BIOLOGY AND CONSERVATION OF THE
Cape (South African) fur seal
Arctocephalus pusillus pusillus
(Pinnipedia: Otariidae)
FROM THE EASTERN CAPE COAST OF SOUTH AFRICA

A thesis submitted for the degree of
Doctor of Philosophy from the
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THE AUSTRALIAN NATIONAL UNIVERSITY

About 200 years ago, the great Swedish naturalist, Carl Von Linné, described the animal group Phoca (=seals) as follows:

> *"This is a dirty, curious, quarrelsome tribe, easily tamed, and polygamous; flesh succulent, tender; fat, and skin useful. They inhabit and swim underwater, and crawl on land with difficulty, because of their retracted fore-feet and united hind-feet; feed on fish and marine productions, and swallow stones to prevent hunger, by distending the stomach".*

Linné, Carl von (1802). *A general system of nature*.....Vol. 1. London: Lackington, Allen. p. 38.

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I declare that the research described in this thesis is my own original work except where otherwise acknowledged. Ten of the thirteen papers presented here are authored jointly with one or more authors. In each case, I am the senior author and the principal contributor to all aspects of the work.

The contribution/s of the co-authors are stated below.

Marthan Bester
(Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa)
Discussion of ideas presented and use of facilities (Chapter 8).

Mike Brett
(Robberg Nature Reserve, Plettenberg Bay, South Africa)
Co-witness to the seal-shark attack. Positive identification of shark species (Chapter 14(b)).

Ansie de Kock and Cecilia Saunders
(Port Elizabeth Technikon Catalysis Research Unit, Port Elizabeth, South Africa)
Analysis of blubber samples for heavy metals and pesticide concentrations (Chapter 12).

Jacobus Fourie
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Positive identification of seal parasites (Chapter 13).

Susan Hemsley and Paul Canfield
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Interpretation of histological slides and contributed to the writing of the publication (Chapter 2).

John Maindonald
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Statistical analysis (Chapter 2).

Mike Meÿer
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Use of supplementary morphometric data from known age seals accessioned at MCM (Chapters 2, 3, 4, 6, 7).

Herman Oosthuizen
(Marine and Coastal Management, Rogge Bay, Cape Town, South Africa)
Use of seal gonads accessioned at MCM (Chapter 8).

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Statistical analysis (Chapters 3, 4, 5, 6, 7).

Stephan Swanson
(Marine and Coastal Management, Rogge Bay, Cape Town, South Africa)
Assisted Mike Meÿer in suture age determination of known age seals accessioned at MCM (Chapter 6).

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Nev Minch and Kay Dancey were responsible for the typesetting of this thesis and Catherine Prvan proof read the final layout. Their services were requested so that the resultant information could be distributed as a WWF educational report to the scientific community, federal, state and local governmental agencies, educational institutions and the public.

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[Note: i. Co-authors and their organisations are thanked individually in the relevant chapters. ii. Key contributors not mentioned above are listed in the acknowledgement section of the relevant chapters]

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(Use of equipment for age determination in seals; use of morphological data from seals of known age; assistance with attachment of satellite transmitters)

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Preface

This thesis is written as a series of thirteen papers (Chapters 2–8, 10, 12–14), plus an introduction (Chapter 1), two unpublished chapters (Chapters 9 and 11) and a conclusion with ideas for future research (Chapter 15). This method of presentation maximises brevity; however, some repetition of methodology and references is inevitable.

Chapters 9 and 11 are currently being prepared for publication. I was unable to finish these two papers in time for inclusion in this thesis.

SUMMARY

Chapter 1: In 1990, the commercial harvest of seals in South Africa was postponed indefinitely until sufficient scientific information was available to make informed management decisions on the issue. Consequently, various programs were initiated on the south-east Atlantic coast, with little work, other than estimation of seal numbers, undertaken on seals of the south-west Indian ocean coast, particularly Algoa Bay, the eastern most boarder of the seals breeding range. Despite the small size of the seal population in this area there is a continuing and increasing interaction between fishermen and seals for available resources. The effects of this on the local seal population are unknown, but unlike the west coast seal population, that on the Eastern Cape coast is not increasing. Subsequently, the World Wide Fund for Nature initiated a study investigating the biology and conservation of Cape fur seals in Eastern Cape waters, to assist in the formulation of policy on seal conservation and management (WWF-South Africa project ZA–348). Specific objectives were to gather information on the: (i) general biology of the species; (ii) impact of commercial harvest; (iii) actual/potential threats that may affect the local seal population; (iv) nature and extent of sea-fisheries interactions; and (v) population size.

Chapter 2: The gross and microscopic anatomy of the Cape fur seal heart, lung, liver, spleen, stomach, intestine and kidneys (n = 31 seals) was described. Data indicate that body weight increased by 23% per annum until at least 9–10 y of age. Organ weight increased at a rate of between 25% and 33% per annum until at least 9–10 y of age, with the exception of the intestines, where exponential increase appeared to have ceased by about 7 y. Most organs increased in proportion to the body. However, the heart, liver and spleen appeared to increase at a faster rate than the body. The basic anatomical features of the viscera were similar to those of other pinnipeds, with some exceptions, including the arrangement of the multilobed lung and liver. Apart from the large liver and kidneys, relative size of the organs did not differ greatly from similar sized terrestrial carnivores. The histological features of the organs were generally consistent with those previously described for this species and other otariids.

Chapter 3: Morphology (n = 12 linear variables), relative size and growth of the male Cape fur seal was described. At birth, males are 35% (*c.* 69 cm) of their mean adult size. At puberty, they are 57% (*c.* 113 cm). The foreflippers are relatively long measuring 25–26% (*c.* 18 cm) of standard body length (SBL) in pups, and 24% (*c.* 48 cm) of SBL in adults. The hind flippers are considerably shorter measuring 19% (*c.* 13 cm) in pups, and 14.5% (*c.* 29 cm) in adults. Axillary girth is usually about 57–67% of SBL. Growth of SBL was rapid during the early postnatal period with a significant growth spurt occurring at the onset of puberty (2–3 y). The rate of growth slowed significantly between 6 and 7 y. A weak growth spurt was observed at 9 and 10 y (social maturity). Growth slowed thereafter, i.e., the mean for males > 10 y was 199 cm. Relative to SBL, facial variables and the fore/hind limbs scaled with negative slope relative to SBL or were negatively allometric; axillary girth scaled with positive slope; and tip of snout to anterior insertion of the foreflipper was positively allometric. Relative to age, body variables scaled with negative slope or were negatively allometric. In animals 1–10 y, SBL was found to be a very ‘rough indicator’ of age and age group.

Chapter 4: Morphology (n = 32 variables), relative size, and growth of the skull was described. Condylobasal length (CBL) was highly, positively correlated with SBL and age. Overall, skull variables grew at a slower rate than SBL, apart from height of mandible at meatus and angularis to coronoideus, which expressed isometry relative to SBL. CBL continued to increase until at least 12 y, with no obvious growth spurt between 8–10 y, when social maturity is attained. Mean CBL was 19.4% of SBL in yearlings; 15.5% in subadults, and 13.7% in adults. Apart from the dentition, all variables of the facial skeleton followed a somatic growth trajectory. Most of these variables expressed positive allometry relative to CBL, with greatest growth occurring in the vertical part of the mandible. Mastoid breadth, and gnathion to middle of occipital crest, expressed a strong secondary growth spurt at 10 y. Breadth of braincase, and basion to bend of pterygoid, followed a neural growth trajectory, scaling with negative slope relative to CBL. Condylobasal length was found to be a ‘rough indicator’ of SBL and age group (adult, subadult), but not of absolute age.

Chapter 5: Morphology (n = 8 linear variables and mass), relative size and growth of the baculum was described. The baculum continued to increase in size until at least 10 y, with growth slowing between 8–10 y, when social maturity is attained. Growth in bacular length, distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width, distal width and proximal shaft height peaked at 10 y. In the largest animals (age unknown), maximum bacular length was 139.3 mm and mass 12.5 g. Relative to SBL, bacular length increased rapidly in young animals, peaked at 9 y (6.9%), and then declined. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length. At 9 y, mean bacular length and mass was 117 mm and 7 g; growth rates in bacular length and mass were 311% and 7125% (relative to age zero), and 5% and 27% (between years); and bacular length averaged 6.9% of SBL. For all males ≥ 12 months, most bacular variables grew at a faster rate than SBL and bacular length. Exceptions included proximal width which was isometric to SBL; distal width and distal shaft height which were isometric to bacular length; and proximal width which was negatively allometric relative to bacular length. Bacular length was found to be a ‘rough indicator’ of SBL and seal age group (pup, yearling, subadult, adult), but not of absolute age.

Chapter 6: Suture age as an indicator of physiological age in the male Cape fur seal was investigated. The sequence of partial suture closure differed from the sequence of full suture closure, with fusion beginning at different ages and some sutures taking longer to close than others. In animals ≤ 12 y, the sequence of full suture closure was the basioccipito-basisphenoid, occipito-parietal, interparietal, coronal and finally the squamosal-jugal. Suture age was found to be an unreliable indicator of chronological age. However, the basioccipito-basisphenoid can be used independently as an indicator of age, i.e., suture open, ≤ 3 y

old; suture fully closed, 3–4 y or older and male has reached puberty.

Chapter 7: Differences in body size and skull morphology (*n* = 31 variables) of male and female Cape fur seals were investigated. Males were found to be significantly larger than females in SBL. Principal component analysis (covariance matrix) showed that the underlying data structure for male and female skull variables was different, and that most variance between the sexes was expressed in overall skull size rather than shape. Males were significantly larger than females in 30 of the 31 skull variables. Breadth of brain case was the same for the genders. Relative to condylobasal length, males were significantly larger than females in 13 of the 30 skull variables. These were gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth, mastoid breadth, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid and height of mandible at meatus. In males, these variables were associated with the acquisition and defence of territory (e.g., large head size and mass; increased structural strength of the skull; increased bite capacity). Females were found to be significantly larger than males, relative to condylobasal length, with respect to breadth of brain case and length of upper postcanine row.

Chapter 8: Reproduction in the male Cape fur seal was investigated. The presence of sperm in the seminiferous and epididymal tubules indicated that males attain puberty between 3 and 4 years of age. Although some males may remain in breeding condition until March, the absence of spermatozoa in the epididymis during February to June, when mean testis mass and mean tubule diameter reached a minimum, clearly showed reproductive quiescence following the rut. Four stages of spermatogenesis were observed: (i) inactive (February/March–June); (ii) early spermatogenesis (July); (iii) late spermatogenesis (July/August–December/January); (iv) epithelial regression (February–June). Individual variation between males, possibly differences in social status and body condition, may influence the duration of spermatogenesis, hence the overlap in duration between epithelial regression and inactivity.

Chapter 9: The diet and foraging behaviour of Cape fur seals from the Eastern Cape coast was investigated. It was shown that Cape fur seals are opportunistic feeders and take predominantly benthic prey. Prey species included 37 species of fish, 7 species of cephalopods, a small number of crustacea (mostly decapoda) and other miscellaneous items. Analysis of faecal samples at the Rondeklippe colony suggested that the most numerous and most frequently occurring prey species were *Cynoglossus zanzibarensis*/*capensis* and *Austroglossus pectoralis*. Analysis of faecal samples (and regurgitates) at Black Rocks seal colony suggested that the most numerous and frequently occurring prey species were *Loligo vulgaris reynaudii* and *Trachurus trachurus capensis*. Analysis of stomach contents from stranded seals suggested that the most important prey species based on percent total mass were *L. vulgaris reynaudii*, *T. trachurus capensis*, *Pagellus bellottii natalensis*, *Etrumeus whiteheadi* and *C. zanzibarensis*/*capensis*. Analysis of stomach contents from animals incidentally entrapped in trawl nets suggested that the most important prey species based on percent total mass were *Lepidopus caudatus*, *M. capensis*/*paradoxus*, *T. trachurus capensis* and *Octopus magnificus*. The model size of *M. capensis, M. paradoxus, T. trachurus capensis, A. pectoralis* and *L. vulgaris reynaudii* consumed by Cape fur seals fell within the range of local commercial catches, indicating potential competition between seals and the fisheries in this region. A bimodal distribution in the frequency of diving at different hours of the day was observed, with most dives occurring near dawn (± 3 hours) and dusk (± 3 hours) (*n* = 2 females). This overlaps with the time of day when important prey species such as *M. capensis, M. paradoxus, T. trachurus capensis* and *L. vulgaris reynaudii* have moved upwards in the water column (away from the sea bed) and are subsequently more accessible to seals. Female Cape fur seals can dive > 160 m, and can remain submerged for at least 3–5 minutes (*n* = 2 females).

Chapter 10: The impact of the fur seal industry on the current distribution and abundance of Cape fur seals in the Eastern Cape coast was investigated. On the Eastern Cape coast, Cape fur seals inhabited six islands in Algoa Bay (Stag, Seal, Black Rocks, St. Croix, Jahleel and Brenton) and two sites in Plettenberg Bay (Seal Point on the Robberg Peninsula and Beacon Island). Soon after British settlement of Algoa Bay in 1820, the St. Croix and Bird Islands were leased to individuals by the governor of the Cape Colony (Lord Charles Sommerset) at an annual rental, for fishing and sealing purposes. Available evidence suggests that seals had been extirpated from St. Croix, Jahleel and Brenton Islands in the late 1850s; Seal Point between 1857 and 1890; Stag Island in the mid/late 1800s; Seal Island in the early 1900s; and Beacon Island in the late 1800s/early 1900s. Black Rocks was the only colony on the Eastern Cape coast to survive commercial sealing operations. Access to Black Rocks is difficult and for that reason sealing activities were irregular. Sealing operations on Black Rocks were terminated in 1949. At present, Black Rocks supports *c.* 700 seals. In the last 12 years the population has decreased by 82%. By destroying seal herds through commercial harvesting, and confining the population to Black Rocks, the population is unable to build up its numbers sufficiently to stimulate colonisation on neighbouring islands. Limited space for breeding seals on Black Rocks, and the influence of storms (gale force winds and high swells) restricts the number of pups that can be reared successfully. It is unlikely that the Black Rocks population can increase quickly enough to flow onto Seal and Stag Island, without being depleted by storms.

Chapter 11(a): An evaluation of operational interactions between the trawl fishing industry and Cape fur seals, in waters off the Eastern Cape coast was conducted. Information was obtained from independent observation aboard commercial trawl vessels. Observations indicated that the annual number of seals entrapped and brought aboard by commercial trawlers was estimated to be 997 (0.258 seals per trawl). The annual mortality rate of seals due to drowning was estimated to be 529 (0.137 seals per trawl). The annual overall mortality rate was estimated to be 549 (0.142 seals drowned/deliberately killed per trawl). Drowned animals were predominantly males, ≥ 5 y. Although the seal population on the Eastern Cape coast remains viable, the long term effects of changing the population structure, by removing males ≥ 5 years, are unknown.

Chapter 11(b): An evaluation of operational interactions between the squid jigging/line fishing industry and Cape fur seals, in waters off the Eastern Cape coast was conducted. Information was obtained from questionnaire surveys, with limited independent observation aboard commercial chokker squid vessels. Fishermen interviewed used various methods to discourage seals from interfering in fishing operations including firing a shot near the seal to frighten it; using clubs; gaffing/hooking the seal; using knives; throwing objects (e.g., sinkers, stones); using a catapult; feeding the seal with mackerel; catching the seal; loud noises; starting of engines; banging gaffs on the water surface; waiting for some other fishermen to shoot the seal; and moving to another area. Some fishermen deliberately kill (shoot) seals in order to reduce their perceived impact. More than 1 000 are illegally shot in this area each year. At sea, it is not always possible to achieve a clean head shot, therefore, many seals are shot in the stomach or back, and die a slow, painful death. Considering that large numbers of seals are being shot in this area, ongoing monitoring of the seal population is required.

Chapter 11(c): The incidence and nature of entanglement of Cape fur seals off the Eastern Cape coast was investigated. Observations during the 1993 pupping season at Black Rocks indicated that the minimum estimated frequency of entanglement was *c*. 0.11–0.22%. Examination of stranding records, animal hospital files, and direct observation at seal colonies, suggested that mono-filament line accounted for 28% of entanglements, trawl net fragments accounted for 36%, and rope accounted for 36% ($n = 26$ entangled seals). Although debris-related mortality does not appear to impact significantly on the local seal population, much of the materials which entangles seals is highly durable, and floats at the water surface for long periods. Such material is likely to accumulate in areas of up- or down- welling where the animals feed. As the fishing industry continues to expand, more synthetic material will accumulate, and the incidence of entanglement in this area will subsequently increase. Therefore continued monitoring of the population, and the nature of entanglement, is essential.

Chapter 12: The concentration of heavy metals (Cd, Cu, Pb, Ni and Zn) and organochlorine contaminants (PCBs, DDT, DDE and DDD) in the blubber of 12 adult male Cape fur seals was investigated. The median and range of concentrations of metals were, in µg/g wet weight: Cd, 0.4 (<0.04–0.53); Cu, 2.6 (2.17–7.43); Pb, 0.7 (0.54–0.99); Ni, 17.7 (9.39–23.18) and Zn, 11.5 (3.14–16.65). Dry weights were: Cd, 0.5 (<0.04–0.59); Cu, 2.9 (2.47–8.45); Pb, 0.6 (0.54–1.14); Ni, 17.0 (10.79–28.22) and Zn, 12.8 (3.61–20.26). Concentrations of Cd, Pb and Zn were in the limits of reported values; however Cu and Ni levels were considerably higher. There was no evidence that the elevated levels of Cu and Ni reported in this study would pose a serious threat to the health of individual animals; however, high concentrations of these metals may be sufficient to result in some additional stress to animals when they mobilise their lipid reserves during illness or starvation. Concentrations of organochlorines (µg/g wet weight) were below the limit of detection.

Chapter 13: Endoparasites recovered from the blubber and stomach of Cape fur seals were documented. Forty three (81%) of the 53 seals examined harboured stomach parasites, and 13 (25%) harboured blubber parasites. Nine parasite taxa were identified. Helminth species included adult cestodes *Diphyllobothrium* sp., larval cestodes, *Hepatoxylon trichiuri* and *Phyllobothrium delphini*; nematodes, *Anisakis physeteris*, *Anisakis simplex*, *Contracaecum ogmorhini*, *Contracaecum* sp. and *Hysterothylacium* sp. and an acanthocephalan, *Corynosoma* sp. Three of these taxa, *Hepatoxylon trichiuri*, *Anisakis physeteris*, and *Hysterothylacium* sp., were accidental parasites. Scanning electron microscope examination confirmed the identity of *Contracaecum ogmorhini* and suggests that earlier studies may have incorrectly identified this nematode as *Contracaecum osculatum*. The endoparasites found in the present study did not appear to contribute to the mortality of Cape fur seals, at least in the population from which the examined specimens were taken. Although the anisakine nematodes, *Contracaecum* sp. and *Anisakis* sp., are potentially pathogenic, severe pathological changes were limited to small gastric lesions in the stomachs of three individuals.

Chapter 14: Preliminary studies investigating the nature and extent of shark predation in Eastern Cape waters were conducted. In Eastern Cape waters, potential shark predators include the white (*Carcharodon carcharias*), broadnose sevengill (*Notorynchus cepedianus*), bluntnose sixgill (*Hexanchus griseus*), shortfin mako (*Isurus oxyrinchus*), bull (*Carcharhinus leucas*), tiger (*Galeocerdo cuvier*), and dusky (*Carcharhinus obscurus*). Only the white and broadnose sevengill shark have been observed actively feeding on Cape fur seals. Shark bitten seals were observed throughout the year, with coastal records peaking in the autumn/winter period. Adult animals were observed with shark bite wounds more often than young. Wounds were usually located on the lower body, suggesting that attacks were made from behind. Fresh shark bite wounds were found on a minimum of 3.4% of seals found stranded on local beaches, and 0.3% of seals observed at the Black Rocks colony during the breeding season. Although predatory encounters appear to be common, long term studies are required before we can fully assess the extent of shark predation along the Eastern Cape coast.

Chapter 15: Immediate threats to the local seal population include deliberate shooting of seals; incidental catch in commercial fishing gear; and storms (gale force winds and high swells) during the pupping/mating season. Commercial harvest was a major threat to the survival of the local population up until 1949. Entanglement in man made debris was identified as a potential threat. Other potential threats, not examined in the present study, included disturbance (e.g., the planned deep sea port and industrial zone within Algoa Bay by Coega Development Corporation), habitat degradation, and episodic mass mortalities. Future research should concentrate on: (i) monitoring of seal numbers; (ii) ways to minimise negative interactions between seals and fisheries; and (iii) monitoring the population for signs of disease. In order to conserve seals in Eastern Cape waters, a comprehensive seal conservation and management plan is required which addresses the following key issues: incidental catch in commercial fishing gear, deliberate shooting of seals, entanglement, disturbance caused by human activity, habitat degradation, episodic mass mortalities, education and marine protected areas.

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CHAPTER 1

Introduction

BACKGROUND OF THE STUDY

The Cape (South African) fur seal, *Arctocephalus pusillus pusillus*, occurs only on the coasts of South Africa and Namibia, and is the only resident seal species in southern Africa. Breeding rookeries are distributed from Black Rocks (33°50'S, 26°16'E) in Algoa Bay, on the south east coast of southern African, to Cape Cross (21°46'S, 13°58'E) in Namibia; however, the species range extends further northward to Cape Frio (18°26'S, 12°00'E) (Fig. 1.1). At the time of this study, the total population was 1.5 to 2 million animals, two-thirds of which were on the Namibian coast (Butterworth & Wickens, 1990; Butterworth & Harwood, 1991) There were 25 breeding colonies (six on the mainland and 19 on small, rocky offshore islands) and an additional ten haul-out sites (six on the mainland and four on islands) (Oosthuizen, 1991[1]). The population was increasing at a rate of 4% per annum (Butterworth *et al.,* 1988).

The Cape fur seal is confined to the continental shelf area and its immediate vicinity. Although seals forage up to 220 km offshore (Warneke & Shaughnessy, 1985), the general foraging area is usually within 93 km of the shore (David, 1987*a*). On the west coast, seals generally remain south of 18°S 12˚E, however some animals disperse northward into the tropics, up to 11°S, assisted by the Benguela Current (Warneke & Shaughnessy, 1985; Oosthuizen 1991). On the east coast, animals seldom range further east than East London (Rand, 1967), with occasional sightings near Durban (29°50'S, 31°00'E) (Gabby Harris, pers. comm.). Although this species is non-migratory, there is considerable movement between colonies, particularly among juveniles (Oosthuizen, 1991). Both sexes travel considerable distances from their colonies to feeding grounds, which are situated mainly between Mossel Bay and Lambert's Bay; Cape Point and Lambert's Bay; north of Luderitz; and north of Cape Cross (Oosthuizen, 1991). Bulls in breeding condition and lactating females feed in the vicinity of their breeding colonies (Shaughnessy, 1981; Oosthuizen, 1991).

The majority of seals occur on the west coast. In this region the cold (10°C to 15°C), slow-flowing, nutrient-rich Benguela Current promotes high primary production and hence large stocks of fish and invertebrates for seals to feed on. The remainder of the population (*c.* 8.5%; 140 000 seals in 1993; J.H.M. David, pers. comm.) inhabits the south/east coast, between False Bay and Algoa Bay, at five breeding[2] colonies and one haul-out site. Three of the five colonies (Geyser Rocks, Quoin Rock and Seal Island-False Bay) are situated west of the Agulhas/ Atlantic mixing area, i.e., in the south-east Atlantic ocean. The remanding three colonies (Seal Island-Mossel Bay, Rondeklippe-Plettenberg Bay and Black Rocks-Algoa Bay) are situated further east, in the south-west Indian ocean, inshore of the warm Agulhas Current (20°C to 25°C) (Rand, 1967). Population estimates for individual breeding colonies have been reported by Shaughnessy (1987, 1993).

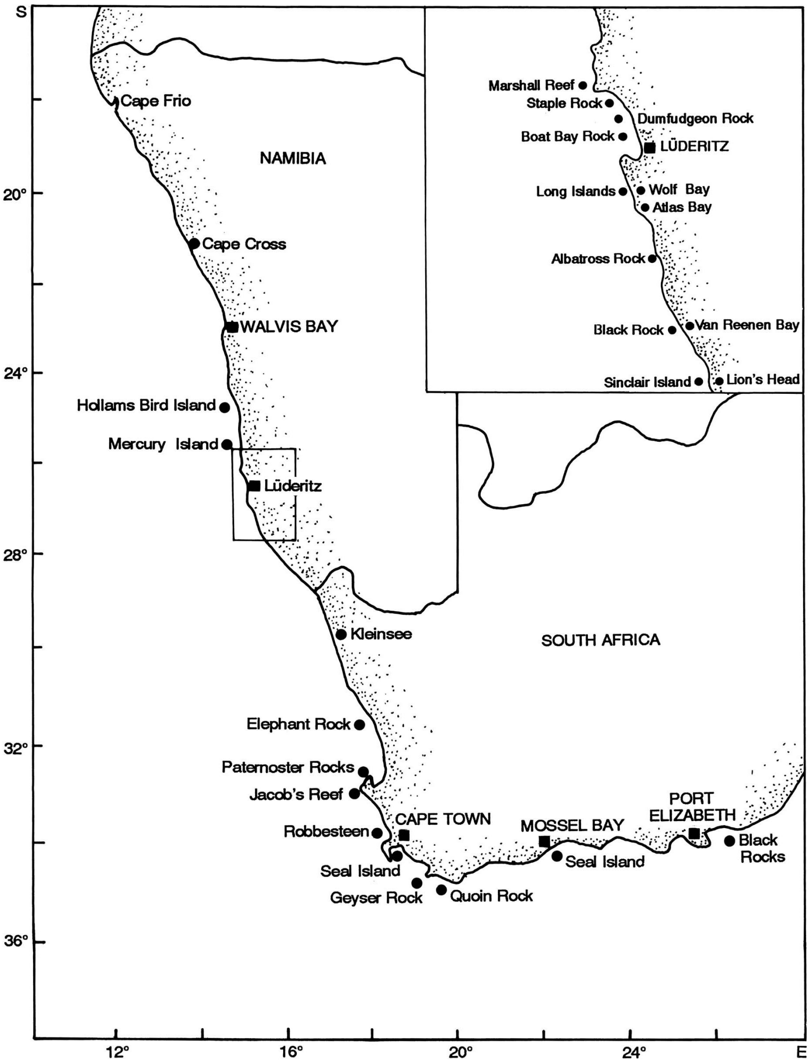

Fig. 1.1 Breeding and non-breeding colonies of the Cape fur seal around the coast of South Africa and Namibia, indicating ICSEAF (International Commission for the Southeast Atlantic Fisheries) areas.
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[1] Refers to the number of colonies for the period 1992 to 1995 when the field work for this study was conducted, and includes the haul-out site at Plettenberg Bay (Rondeklippe).

[2] A seal colony is classified as a breeding colony when 1000 pups are born annually at that site.

Since 1610, Cape fur seals have been exploited by Europeans primarily for their fine quality furs. Rookeries were invaded throughout the year and animals slaughtered irrespective of sex and age class. By the end of the 19th century, seal numbers had been reduced to very low levels, i.e., < 100 000 animals. More than 20 island colonies had been extirpated. Subsequently, in 1893, the first legal restrictions over sealing in southern Africa were introduced (Cape Fish Protection Act) which prohibited commercial sealers from operating without a government permit. In 1909, harvesting of seals during the breeding season was prohibited. Sealing activities along the Namibian coast were not regulated until 1922 (Sealing and Fishing Proclamation), with additional restrictions introduced in 1949 (Sealing and Fisheries Ordinance). Both acts prohibited sealing without a licence (Shaughnessy, 1984; David, 1987*a*). Since 1973, sealing has been managed under the Sea Birds and Seals Protection Act. Permits issued under this Act specify the age, size and sex of seals killed; and the season and area where sealing may take place. Subsequent to this Act, seals have been exploited on a sustainable basis and seal numbers have been increasing steadily (Butterworth *et al.,* 1988).

Growth in the seal population has coincided with a decline in commercial catches in many sectors of the fishing industry. Some of the species eaten by seals are of commercial importance, therefore it is inevitable that seals and fisheries will come into conflict when fishing (= operational interactions) (Rand, 1959; Shaughnessy & Payne, 1979; Shaughnessy, 1980; Shaughnessy *et al.,* 1981; Shaughnessy, 1985; Anon., 1987, 1990*a*, *b*; David, 1987*b*; Butterworth *et al.,* 1988; Wickens, 1989). Consequences of interactions with the fisheries include: consumption of catches, disturbance of fishing operations and damage to gear. Consequences to seals include: deliberate shooting of seals, drowning in nets and entanglement in discarded fishing gear. Apart from conflicts during fishing operations, many commercial fishermen believe that seals consume substantial quantities of fish that would otherwise be available to the industry (= biological interactions). This unsubstantiated belief is based on two facts–seals eat fish and occur in the region where the fishery operates.

In 1986, a Commission of Enquiry into the Fishing Industry recommended that seals be culled in order to reduce the number of fish consumed by seals, thereby increasing the availability of fish to the industry (Anon., 1986; Diemont, 1986). Three years before this recommendation, the seal industry had crashed due to intense lobbying by conservation organisations in North America and Europe. Conservationists wanted the harvest to stop primarily for emotional and humanitarian reasons. This removed much of the commercial incentive for harvesting seals in southern Africa, and focused considerable international media attention on the culling debate. Since 1900, more than 2.5 million pups and bulls had been harvested in southern Africa.

In response to international pressure in 1990, the annual harvest of Cape fur seals in South Africa was postponed indefinitely until sufficient scientific information was available to make informed management decisions on the issue. This decision was based on the recommendations of an Advisory Committee (chaired by Dr John Hanks, WWF) appointed to counsel the Minister of Environment Affairs on the scientific aspects sealing. The committee concluded that there was “no scientific basis for culling”. This decision was largely based on the research of Butterworth *et. al.,* (1988); Wickens (1989); Butterworth & Harwood (1991) and several anonymous reports (Anon., 1983, 1987, 1990*a*).

Consequently, various programs were initiated by Marine and Coastal Management (formerly Sea Fisheries Research Institute) to gather information on seal biology, population numbers, and seal-fisheries interactions for management. The majority of research was concentrated on seals inhabiting the south-east Atlantic coast, with little work, other than estimation of seal numbers, undertaken on seals of the south-west Indian ocean coast, particularly Algoa Bay, the eastern most boarder of the seals breeding range. Despite the small size of the seal population in this area, there is a continuing and increasing interaction between fishermen and seals for available resources, particularly that for line fish and chokker squid, the value of which, in combination, exceeds R100 million annually (e.g., from 1993–1995, white squid grossed between R112,646,538.00–R118,909,710.00 per annum and line fish grossed between R9,459,522.00–12,052,005.00 per annum[3]; Chris Wilke, pers. comm.). The effects of this on the local seal population are unknown, but unlike the west coast population, that on the Eastern Cape coast is not increasing.

Therefore, in 1992, a research program was initiated to examine the biology and conservation of Cape fur seals in the Eastern Cape (WWF project ZA–348). The program was based at the Port Elizabeth Museum, and funded by World Wide Fund for Nature – South Africa, in association with Total-South Africa. I was appointed project executant. Data collected from this program formed the basis of my PhD.

Specific objectives of the Eastern Cape seal study were to gather information on:
(i) general biology of the species.
(ii) impact of commercial harvest on the current distribution and abundance patterns of the local seal population.
(iii) actual/potential threats that may affect the local seal population.
(iv) nature and extent of seal-fisheries interactions in the region.
(v) population size.

Field studies were completed within a limited period of 4 years (May 1992 to August 1995).

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[3] Gross earnings are for Port Alfred to Mossel Bay for the period 1993–1995.

This thesis reports on my research into the biology and conservation of the Cape fur seal from the Eastern Cape coast of South Africa. The first section of the thesis (chapters 2–9) documents the general biology of Cape fur seals. In chapter 2, gross and microscopic visceral anatomy of the male is described and the relationship between organ weight and age investigated. Chapters 3–5 describe the general morphology (body, skull and baculum) of the male. Growth relative to standard body length and age is examined, and age at social maturity established. In chapter 6, information on asymptotic size inferred from physiological (suture) age is presented. Sexual dimorphism is examined in chapter 7. In chapter 8, reproduction in the male is investigated and age at puberty established. Reproduction in the female has been examined previously (Rand, 1955; Warneke & Shaughnessy, 1985; David & Rand, 1986) and was therefore not investigated here. Chapter 9 investigates diet and foraging behaviour of the local seal population.

The second section of the thesis, conservation biology (chapters 10–14), investigates actual/potential threats that may influence the future status of the local seal population, and provides estimates of population size. Chapter 10 investigates the impact of commercial harvest on the current distribution and abundance patterns of the local seal population. In chapter 11, the nature and extent of seal-fisheries operational interactions are investigated. Information on direct killing of seals by fishermen, incidental catch in fishing nets and entanglement in discarded fishing gear is presented, and the impact of seals on fisheries accessed. Chapter 12 documents the concentrations of heavy metals and organochlorine contaminants in the blubber of seals. In chapter 13, information on endoparasites in the stomach and blubber of seals is presented, and evidence of pathological manifestations assessed. Shark predation on the local seal populations is examined in chapter 14

In the final chapter, I present the conclusions of the study, and specify areas where further research is needed to assist in the future management of this species in the Eastern Cape coast.

THE STUDY AREA

The Eastern Cape coast extends from Robberg, Plettenberg Bay (33°07'S, 23°25'E) to the Kwazulu-Natal boarder (31°05'S, 30°11'E), encompassing *c.* 800 km of coast-line (Fig 1.2). Considering that Cape fur seals are seldom seen further north than East London, field studies were conducted between Plettenberg Bay and East London, with much of the work concentrated within Algoa Bay.

Seal colonies

There are two seals colonies in the Eastern Cape, a breeding colony at Black Rocks, Algoa Bay, and a small non-breeding colony at Robberg (Rondeklippe), Plettenberg Bay (33°06'S, 23°24'E) (Fig. 1.2).

Black Rocks consists of five small rocky outcrops composed of quartzitic sandstones of the Table Mountain Group (Council for Geoscience, pers. comm.). The outcrops are partially joined together by a reef of drying and submerged rocks. They are situated 8–9 km off-shore (not sheltered by headlands); small in size (the largest rocky outcrop is 8 360 m^2); low-lying (the largest outcrop is 6 m above mean sea level); and often surrounded by heavy breakers (Rand, 1963, 1972; Chart SAN 1025). Water depth is *c.* 30 m (Bremner, 1991a). In 1992 the estimated seal population was 2 315 seals, and in 1996 it was 1 480 seals (Marine & Coastal Management, Unpubl. data).

Rondeklippe consists of a rocky platform composed of quartzitic sandstones of the Robberg Formation (Council for Geoscience, pers. comm.). The rocky platform covers an area *c.* 240 m^2. The highest point is *c.* 2.8 m above mean sea level. Water depth is 3.5 m. From 1992 to 1996, seal numbers increased from *c.* 12 to *c.* 50.

Seal Island, Mossel Bay (34°09'S, 22°07'E), lies to the west of Plettenberg Bay, just outside the study area. In 1992 the estimated seal population was 3 770 seals, and in 1996 it was 4 945 seals (Marine & Coastal Management, Unpubl. data).

Although it is probable that the seals along the east coast share feeding grounds, the extent of movement between the three colonies is not known.

Coastal and bottom topography

Algoa Bay is a large, crenulated embayment facing the south-west Indian ocean, on the south east coast of South Africa (Goschen & Schumann, 1988). Cape Recife forms the western boundary of Algoa Bay, and the less prominent Cape Padrone forms the eastern boundary, with the port installations and the city of Port Elizabeth in the western section. Large columns of fresh water flow offshore from the Swartkops, Coega, and Sundays rivers.

There are five separate areas of Palaeozoic outcrop within Algoa Bay: (i) the inner shelf south of Cape Recife; (ii) Riy Bank; (iii) the Bird Island complex (Bird, Stag and Seal Islands; Black Rocks); (iv) the St Croix islands (St Croix Island; Jahleel and Brenton Islets) including the mouth of the Coega River; and (v) off Cape Padrone. Three of these outcrops (Cape Recife, Riy Bank and the flanks of Bird Island) are linked by a ridge known as the Recife-Bird

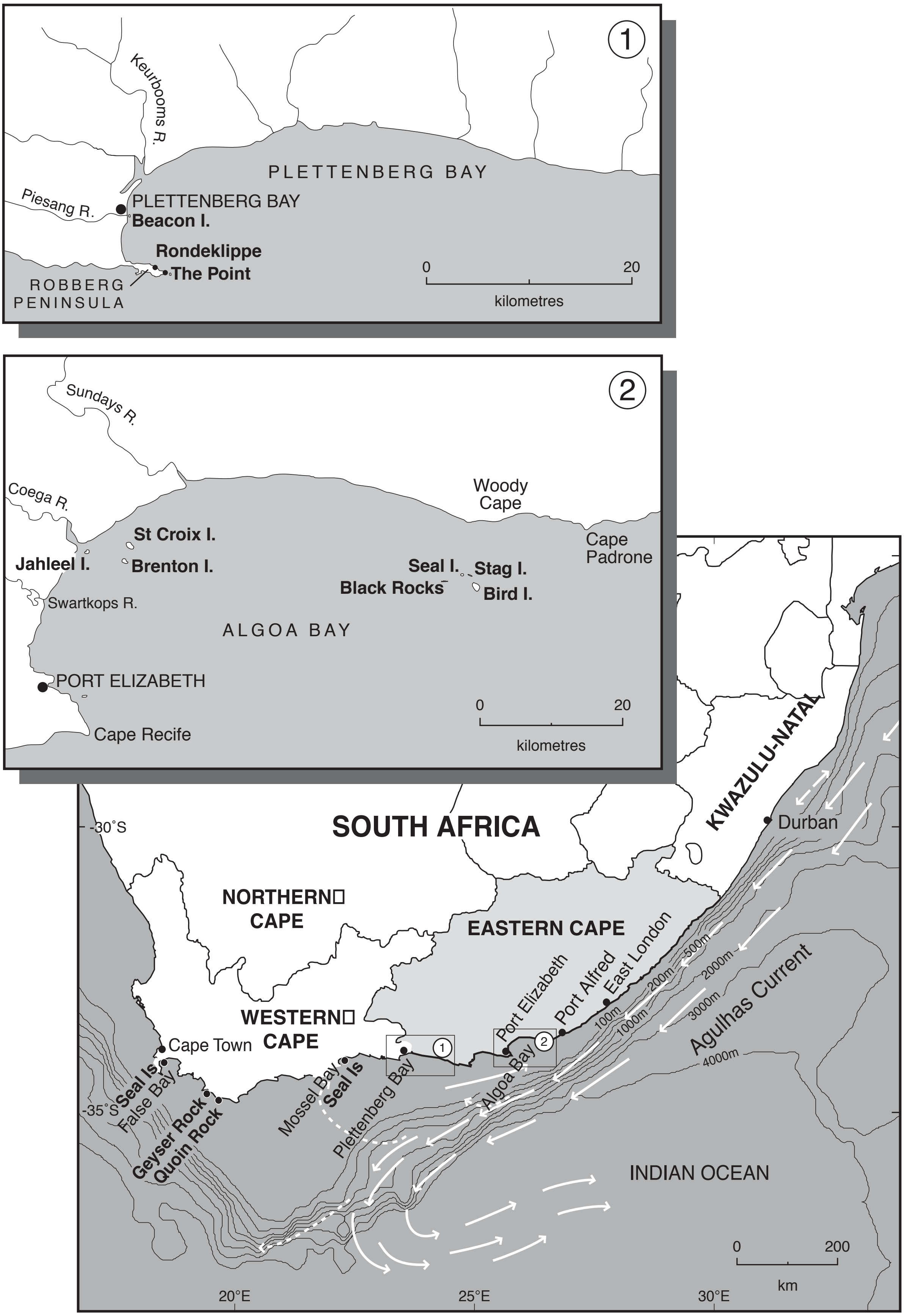

Fig. 1.2 The distribution of Cape fur seals along the Eastern Cape coast of southern Africa, indicating the breeding colony at Black Rocks (Algoa Bay), and the haul-out site at Rondeklippe (Plettenberg Bay).

Ridge (Bremner & Day, 1991). Sand flats occur underwater between reefs.

The coast-line to the west of Algoa Bay consists of a series of large, warm, sheltered bays (Plettenberg, Mossel, Jeffreys, and Cape St Francis) connected by stretches of open rocky shore. Approximate water depth at the outer extremities of these bays is: Plettenberg Bay < 60 m; Mossel Bay < 50 m; Jeffreys and Cape St Francis combined < 70 m (Council for Geoscience, pers. comm.).

The coast-line to the north-east of Algoa Bay straightens out progressively and is therefore less sheltered. Along this stretch of coast, the 50 m isobath contour lies *c.* 2.4–5.6 km offshore, e.g., *c.* 5.6 km from the coast-line at Kenton-on-sea; *c.* 4.6 km from the coast-line at Port Alfred; 2.8 km from the coast-line at Great Fish Point; from the coast-line at Keiskamma Point (3.7 km); and from the coast-line at East London Light House (2.4 km) (Council for Geoscience, pers. comm.).

The continental shelf (200 m isobath contour) lies *c.* 228 km from the coast-line off Cape Agulhas (at its widest point south of the Agulhas Bank); *c.* 96 km from the coast-line off Plettenberg Bay; *c.* 44.5 km from the coast-line off Port Elizabeth Lighthouse; and *c.* 24.1 km from the coast-line off East London (Council for Geoscience, pers. comm.).

Hydrological features

Agulhas Current

The most prominent oceanic feature of the study area is the Agulhas Current which originates from the Mozambique Current and the East Madagascar Current. The Agulhas Current forms between southern Mozambique and Durban (25°S–30°S). It is deep, narrow and fast-flowing, transporting 70–80 million cubic metres of water each second, with an average surface speed of 1–2 $m.s^{-1}$ (Shannon, 1989). Surface temperature varies seasonally between 22°C in August (winter) and 27°C in March (autumn) (Heydorn *et al.,* 1978). Central Water lies beneath the current in depths of 200 m to 800 m, and its temperature and salinity decrease with depth (Heydorn *et al.,* 1978).

The Agulhas Current flows in a south-westerly direction along the coast, roughly following the edge of the continental shelf. The inner boundary of the current is usually located above the 200 m isobath contour. Between Durban and East London the shelf is narrow, therefore the current flows close to the shore. Between East London and Port Elizabeth the shelf broadens, therefore, the current begins to diverge from the coast. It then veers south before reaching the Agulhas Bank. The current becomes an 'unstable jet' 350 to 400 km offshore (Harris, 1978) and then turns back on itself in an anticlockwise direction to form the Agulhas Return Current.

There is no direct and continuous flow of warm Agulhas water into the south-east Atlantic ocean. However, west of Algoa Bay, meanders and frontal eddies of the Agulhas Current increase in dimension (Goschen, 1991). Plumes of warmer water attached to eddies may cross the shelf edge, advecting warmer, high-salinity water (24°C^{+}) over the Agulhas Bank (Eagle & Orren, 1985; Swart & Largier, 1987; Goschen & Schumann, 1988; Lutjeharms, 1981; Dr Ian Hunter, pers. comm.).

The Agulhas Current supports a diverse range of fish species; however, fish abundance is considerably less than that on the west coast. The reason for this is because the surface waters of the Agulhas Current originate in warm tropical regions; and are low in nutrients and oxygen (Shillington, 1986).

Wind induced upwelling

Water movement in the near-shore region of Algoa Bay is mainly due to wind forcing (Roberts, 1990). At the Bird Islands, the prevailing winds (W–SW and E–NE) are parallel with the general orientation of the coast (Illenberger 1986; Goschen, 1988, 1991; Schumann & Martin, 1991). Westerly-component winds are common for most of the year, with easterly-component winds dominant in summer (Schumann, 1992).

In summer, easterly component winds increase in strength and frequency causing localised up-welling at the major Capes and a subsequent fall is SST (Schumann, Ross & Goschen, 1988; Goschen, 1991). Localised up-welling enhances primary productivity by bringing nutrient salts into the euphotic zone, promoting the growth of plankton which indirectly benefits large predators by increasing prey availability. In winter, the frequency of easterly-component winds decreases, and the depth of the surface isothermal layer over the shelf increases, resulting in a reduction in wind driven up-welling (Goschen, 1991).

Sea surface temperature

Temperature structure within Algoa Bay is caused by seasonal variability in the surface heat fluxes and mass transports of water (Goschen, 1991). SST's decrease from the shoreline to the shelf, and then increase again to the Agulhas Current (Goschen, 1991). A strong thermocline (surface layer 15°C to 20°C; bottom layer 9°C to 12°C) is present over the continental shelf off Algoa Bay (Goschen, 1991). However, the shallow inshore waters are generally well mixed due to wind-forcing (Goschen & Schumann, 1988).

At Black Rock seal colony, daily SST ranges from 12°C to 23°C, with mean monthly temperatures peaking in January/February (19°C), and reaching a low in July–October (16°C) (Appendix A).

At Plettenberg Bay, daily SST ranges from 10°C to 24°C, with mean monthly temperatures peaking in summer (22°C), and reaching a low in winter (15.8°C) (Chantal Greenwood, pers. comm.).

At East London, daily SST ranges from 12.5°C to 22.5°C, with mean monthly temperatures peaking in summer (19°C), and reaching a low in winter/early spring (17.0°C to 17.5°C) (Chantal Greenwood, pers. comm.).

Swell

The most common swell along the Eastern Cape coast is from the south-west, usually originating from low pressure systems moving from west to east over the southern ocean. Abnormal waves, with amplitudes in excess of 18 m, occasionally occur along the shelf break, and waves around 10 m or more occasionally enter Algoa Bay (Bremner, 1991*b*).

Air temperature

At the Black Rock seal colony, daily air temperature ranges from 9°C to 33°C, with mean monthly temperatures peaking in January/February (26°C), and reaching a low in winter and early/mid spring (21°C to 22°C) (Appendix A).

At Storms River mouth near Plettenberg Bay, daily air temperature ranges from 5.3°C to 41.7°C, with mean monthly temperatures peaking in January/February (22.0°C to 22.1°C), and reaching a low in July (15.6°C) (Chantal Greenwood, pers. comm.).

At East London, daily air temperature ranges from 2.2°C to 38.7°C, with mean monthly temperatures peaking in January/February (23.7°C to 23.9°C), and reaching a low in July (11.5°C) (Chantal Greenwood, pers. comm.).

STUDY ANIMAL

The Cape fur seal is a large, amphibious marine mammal, inhabiting cool coastal waters. Information on the general morphology and natural history of this species is summarised in Table 1.1.

Table 1.1 *South African (Cape) fur seal fact sheet*

Classification	
Family	Otariidae
Superfamily	Arctocephalinae (fur seals)
Species	*Arctocephalus pusillus* (Schreber, 1776)
Subspecies	*Arctocephalus pusillus pusillus* (Schreber, 1776)
Description	
New born pups	Colour: velvety black Length: 60–80 cm. Weigh: 5–6 kg.
Adult males	Colour: dark blackish-grey dorsally; lighter ventrally Length: up to 234 cm. Weight: up to 360 kg.
Adult females	Colour: brownish-grey dorsally; light brown ventrally Length: up to 176 cm. Weight: up to 122 kg.
Reproduction	
Breeding system	Polygynous (mean size of harems: 28 females)
First parturition	4–5 yrs
Age when males attain territorial status	8–13 yrs
Pupping/mating season	Late October to late December
Gestation	Twelve months (delay of implantation of 3.5–4 months)
No. of offspring	One pup each year (twins rare)
Weaning	Usually 8–10 months (up to 12 months or longer)
Breeding habitat	Small, rocky offshore islands and sand beaches on the mainland
Longevity	Few reach 25 yrs of age in the wild (females live slightly longer than males)
Diet	Primarily fish and cephalopods (mainly squid)
Predators	Black backed jackals, brown hyenas, sharks and killer whales
Population size	1.5 to 2 million
Distribution	Namibia and South Africa
Migration	Non-migratory but disperses over long distances
Conservation status	Protected under the Sea Birds and Seals Protection Act of 1973

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PLATES 1–5

Plate 1(a) Cape fur seals at Black Rocks, Algoa Bay

1.1

1.2

1.1 Aerial view of the main breeding rock (photo: C. Stewardson).
1.2 Large males in breeding condition; mature females; black pups (photo: C. Stewardson).

Plate 1(b) Cape fur seals at Black Rocks, Algoa Bay

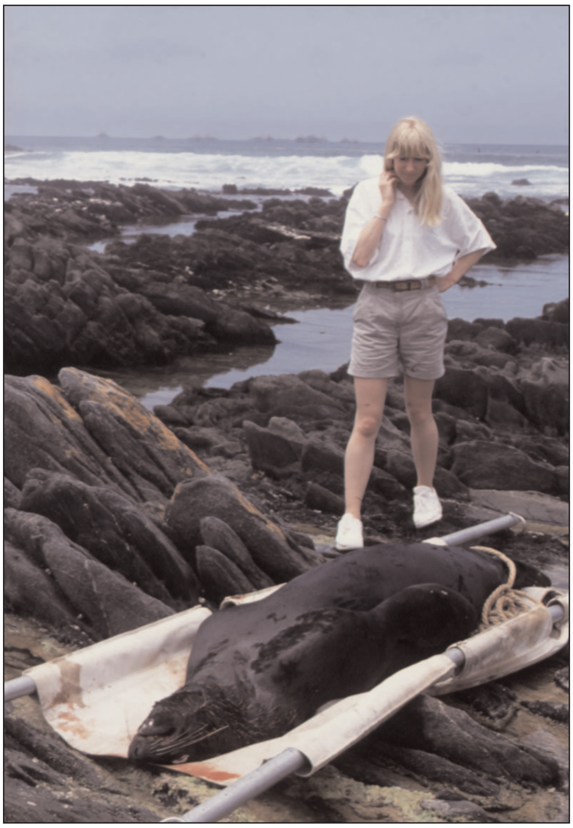
1.3

1.4

1.3 Mature female-note light chest and throat (photo: C. Urquhart).
1.4 Group of seals basking in the sun after returning from a swim (photo: C. Urquhart).

Plate 2 Collection of biological specimens

2.1



2.2

2.3

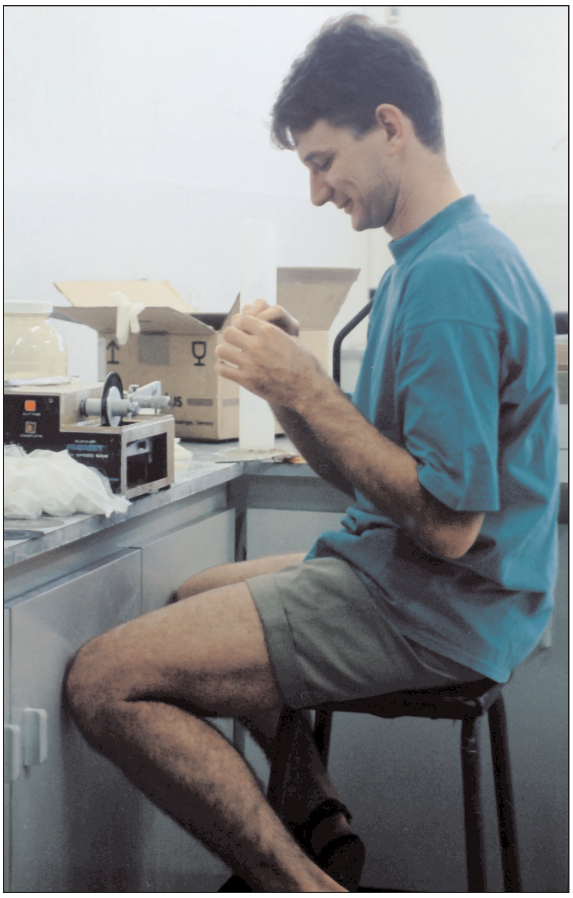
2.1 Seals collected for this study were obtained by non-lethal means, e.g., seals found stranded on local beaches (photo: C. Stewardson).

2.2. Seals were brought back to the Port Elizabeth Museum for biological examination. This seal was shot by squid fisherman (photo: C. Urquhart).

2.3 Post mortem examination, i.e., standard measurements were taken and biological material collected (photo: L. Karczmarski).

Plate 3 Age determination

3.1



3.2

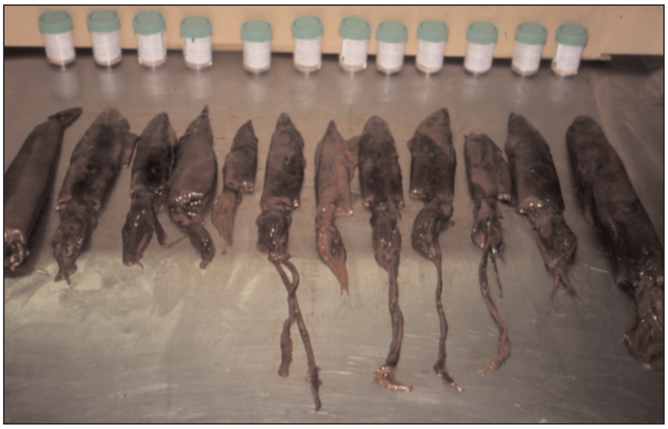
3.3

3.1 Upper canines were removed from the skull, mounted on aluminium chunks, and cut either side of the mid-line using a circular saw fitted with a diamond wafering blade (photo: A. Stewardson).

3.2 Longitudinal sections were then ground down to 280–320 µm (photo: C. Stewardson).

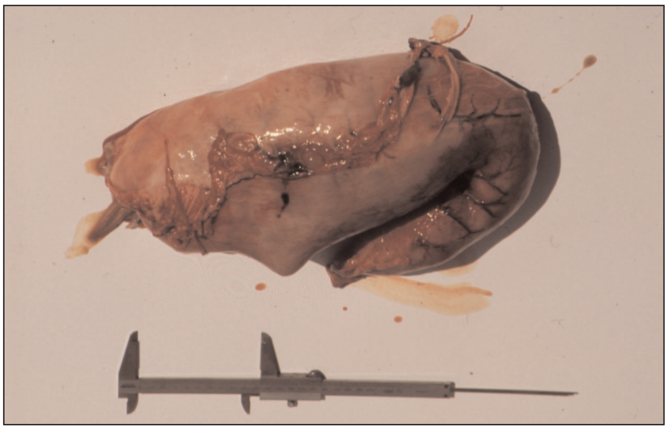
3.3 Sections were dehydrated, mounted, and viewed under a steriomicroscope in polarised light. The number of incremental lines in the dentine were counted and ages rounded off to the closest birth date, i.e., 1 December (photo: compliments SFRI).

Plate 4 Diet inferred from stomach analysis



4.3

4.4



4.1

4.2

4.1 Stomach from a Cape fur seal (photo: C. Stewardson).

4.2 Mackerel (*Scomber japonicus*) recovered from the stomach of a seal that had drowned in a trawl net (photo: C. Stewardson).

4.3 Chokka squid (*Loligo vulgaris*) recovered from the stomach of a seal that had been shot by fisherman (photo: C. Stewardson).

4.4 Seal prey items were positively identified using the Port Elizabeth Museum squid and otolith collections (photo: L. Karczmarski).

Plate 5(a) Foraging behaviour investigated using satellite telemetry

5.1

5.2

5.1 Seal capture team carry hoop net and harness board onto Black Rocks (photo: C. Urquhart).

5.2 Adult female is captured and restrained. A patch of fur on her back (mid-line behind the shoulders) is washed in acetone before attaching the satellite-linked-time-depth recorder (SLTDR) (photo: C. Urquhart).

Plate 5(b) Foraging behaviour investigated using satellite telemetry

5.3

5.4

5.3 The SLTDR is glued onto the fur using devcon 5-minute epoxy 14270 (photo: C. Urquhart).
5.4 Close up of the SLTDR attached to the adult female (photo: C. Urquhart).

PART 1

GENERAL BIOLOGY

VISCERAL ANATOMY

CHAPTER 2

Gross and microscopic visceral anatomy of the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae), with reference to organ size and growth

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ABSTRACT

The gross and microscopic anatomy of the Cape fur seal heart, lung, liver, spleen, stomach, intestine and kidneys (n = 31 seals) is described. Absolute and relative size of organs from 30 male seals are presented, with histological examination conducted on 7 animals. The relationship between log body weight, log organ weight and age was investigated using linear regression. Twenty five animals were of known age, while 6 were aged from counts of incremental lines observed in the dentine of tooth sections. For the range of ages represented in this study, body weight changes were accurately described by the exponential growth equation, weight = $w_o r^t$, with body weight increasing by 23% per annum until at least 9–10 y of age. Organ weight increased at a rate of between 25% and 33% per annum until at least 9–10 y of age, with the exception of the intestines, where exponential increase appeared to have ceased by about 7 y. The relationship between body weight and organ weight was investigated using logarithmic transformations of the allometric equation, $y = ax^b$, where the exponent b is 1 if organ weight is proportional to body weight. Most organs increased in proportion to the body. However, the heart, liver and spleen had exponents $b > 1$, suggesting that these organs increased at a faster rate than the body. The basic anatomical features of the viscera were similar to those of other pinnipeds, with some exceptions, including the arrangement of the multilobed lung and liver. Apart from the large liver and kidneys, relative size of the organs did not differ greatly from similar sized terrestrial carnivores. The histological features of the organs were generally consistent with those previously described for this species and other otariids. The heart, as in other pinnipeds, was unlike that of cetacea in not having unusually thick endocardium or prominent Purkinje cells. Notable histological features of the lungs included prominent fibrous septa, prominent smooth muscle bundles, cartilage extending to the level of the alveolar sacs and ample lymphoid tissue. The spleen had a thick capsule, well developed trabeculae and plentiful plasma cells. Abundant parietal cells were present in the fundic glands and lymphoid follicles were present in the gastric lamina propria, particularly in the pyloric region. Small intestinal villi were very long but this could have resulted from underlying chronic inflammation. Lymphoid follicles were prominent in the colon. The kidney reniculi each had a complete cortex, medulla and calyx, but a sporta peri medullaris musculosa was not identified.

Key words: Pinnipeds, organ growth, allometry

INTRODUCTION

Little research has been carried out on the gross visceral anatomy of the Otariidae. Early descriptions have concentrated largely on the California sea lion, *Zalophus californianus*, and the South American sea lion, *Otaria byronia* (Murie, 1874; Green, 1972; Odell, 1981; Vaz-Ferreira, 1981); while histological studies have mainly concentrated on the California sea lion and the Steller sea lion, *Eumetopias jubatus* (Simpson & Gardner, 1972). Information for the southern fur seals, *Arctocephalus* spp., is scant. Apart from organ weights, no attempt has been made to describe the gross visceral anatomy of this genus. Published information on histological features of southern fur seals is limited to a study of the kidneys of 6 Cape fur seals, *Arctocephalus pusillus pusillus* (Bester, 1975), the lung of 1 Cape fur seal (Denison & Kooyman, 1973), and the spleen of 1 Antarctic fur seal, *Arctocephalus gazella* (Schumacher & Welsch, 1987).

Information on size and relative weights of the viscera has been published for several species of otariids, including the California sea lion (Forbes, 1882), Steller sea lion (Engle, 1926), northern fur seal, *Callorhinus ursinus* (Scheffer, 1960), New Zealand sea lion, *Phocarctos hookeri* (King, 1983), New Zealand fur seal, *Arctocephalus forsteri* (Miller, 1975), subantarctic fur seal, *Arctocephalus tropicalis* (Bonner, 1968), and the Antarctic fur seal (Bonner, 1968; Payne, 1979). However, most of these records are incomplete. Apart from studies conducted by Bryden (1972) and Payne (1979), few organ types have been examined and very little is known of the relative weights of organs at different age groups.

In this paper, we describe the gross and microscopic anatomy of the male Cape fur seal heart, lung, liver, spleen, stomach, intestine and kidneys. Absolute and relative size of organs from 30 seals are presented, with histological examination conducted on 7 animals ($n = 31$ seals). The relationship between log body weight, log organ weight and age was investigated using linear regression.

MATERIALS AND METHODS

Animals

The Cape fur seal breeds at 25 colonies distributed from Black Rocks (lat. 33° 50’S, long. 26°15’E) on the south-east coast of South Africa, to Cape Cross (lat. 21° 46’S, long. 13° 57’E), Namibia. Males are weaned at 6 to 12 months of age (Warneke & Shaughnessy, 1985; David, 1987), attain puberty between 3 and 4 y of age (Stewardson *et al*., 1998) and are able to hold territories when aged *c.* 10–14 y of age (David, 1989). They are considerably larger than females and attain an average length and weight of 217 cm and 174 kg respectively (Warneke & Shaughnessy, 1985). Estimated longevity is at least 20 y (Wickens, 1993).

Thirty-one Cape fur seals were included in this study (Table 2.1). These animals were inadvertently drowned within trawl nets during commercial fishing operations off the coast of southern Africa. Exceptions included 1 juvenile that died of head injuries (PEM2198), and a 2nd juvenile collected under scientific permit (AP5162). Animals were collected in the area 32°–36°S and 17°–24°E, between June 1986 and May 1998. Twenty five seals were of known-age, while 6 were aged from incremental lines observed in the dentine of tooth sections. Organ weights were taken from every animal, except AP5162. Seven of these animals were immediately placed on ice and brought back to a laboratory within 36 h of death for dissection and histological fixation: 2 juveniles (AP5162; PEM2198), 2 subadult (PEM 2257a; PEM2253) and 3 adult seals (PEM2400; PEM 2257b; PEM2348). PEM2198 was frozen prior to dissection.

Morphometry

Standard necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). Standard body length was measured in a straight line from the tip of the snout to the tip of the tail, with the unskinned animal lying on its back. Blubber measurements were taken at the base of the sternum. Upper canines were collected for age determination. Body organs, including the heart, lung, liver, spleen, stomach, intestine and kidneys, were excised and examined directly. Before the organs were weighed, blood was removed from the heart and the stomach washed. The intestine was separated from the mesentery, laid out horizontally, and total length measured. The intestines were weighed full. Lung weights included the trachea and bronchi. Organs were weighed using a beam or electronic balance, and measurements were taken to the nearest 5 mm using a flexible tape measure or vernier callipers as appropriate.

The relationship between body weight and organ weight was investigated using the logarithmic (base *e*) transformation of the allometric equation, $y = ax^b$, where y = organ weight (g); x = body weight (kg); a = proportionality coefficient ($y = a$ when $x = 1$); exponent = b (Schmidt-Nielsen, 1984). The equation may equivalently be written:

$$\log y = \log a + b \log x$$
$$= a' + b \log x$$

and this form can be fitted using straight line regression, where now b can be estimated as the slope of the regression line. We have used ‘robust’ variant of straight line regression, implemented in S-PLUS (Chambers & Hastie, 1991). This gives a reduced weight to data points which lie well away from the line.

The relationship between body weight and age (y) was investigated using the exponential growth equation, weight = $w_o r^t$, where w_o = weight at time zero;

Table 2.1 ***Details of 31 male Cape fur seals caught off the coast of southern Africa***

Accession no.[a]	Date	Age[b]	SBL[c] (cm)	Weight (kg)	Girth (cm)	Blubber[d] (cm)
AP5162	**21 May 98**	**6mo**	**90**	**16**	**64**	—
AP5001	1 Oct 96	10 mo	96	24	75	2.7
AP5000	1 Oct 96	10 mo	96	22	67	2.3
AP4998	7 Oct 96	10 mo	93	18	61	2.0
PEM2198	**6 July 94**	**1 y**	**104**	**28**	**67**	—
AP5134	22 May 97	1 y 6 mo	97	24	66	2.3
AP4985	26 June 96	1 y 7 mo	92	19	59	1.5
AP5005	18 Oct 96	1 y 11 mo	91	18	57	1.0
AP4023	28 June 89	2 y 7 mo	113	34	75	1.3
AP4991	15 Aug 96	2 y 9 mo	102	29	67	1.0
AP5142	19 Aug 97	2 y 9 mo	107	28	72	2.0
AP5135	23 July 97	3 y 8 mo	110	36	78	1.7
AP4996	28 Sep 96	3 y 10 mo	115	30	70	1.7
AP5002	6 Oct 96	3 y 10 mo	108	33	72	1.8
AP4584	19 Jan 95	4 y 2 mo	125	42	81	2.3
AP4585	19 Jan 95	4 y 2 mo	152	38	79	1.3
AP5022	26 Nov 96	5 y	139	55	85	1.2
AP4595	17 Oct 95	4 y 11 mo	134	51	87	1.4
AP3582	6 June 86	5 y 6 mo	142	58	90	3.0
AP3589	12 Aug 86	5 y 8 mo	148	68	98	2.3
AP4987	5 Aug 96	5 y 8 mo	144	54	88	1.7
PEM2257a	**19 Sep 94**	**6 y**	**142**	**73**	**93**	**1.7**
AP5021	26 Dec 96	6 y 1 mo	141	55	90	0.9
AP5133	14 Jan 97	6 y 1 mo	153	69	88	0.8
AP5136	15 July 97	6 y 8 mo	149	74	98	2.3
PEM2253	**27 Aug 94**	**7 y**	**152**	**86**	**128**	**4.0**
PEM2400	**13 July 95**	**8 y**	**176**	**97**	**102**	**2.9**
AP4597	15 Sep 95	8 y 10 mo	170	101	109	2.4
PEM2257b	**7 Oct 94**	**9 y**	**170**	**128**	**120**	**4.0**
AP4992	13 Sep 96	9 y 10 mo	165	95	107	2.3
PEM2348	**14 Nov 94**	**10 y**	**189**	**179**	**97**	**3.3**

[a] AP, Sea Fisheries Research Institute, seal accession number; PEM, Port Elizabeth Museum, seal accession number.
[b] Age in months and years.
[c] Standard body length, i.e., straight line from the tip of the snout to the tip of the tail, with the unskinned animal lying on its back.
[d] Blubber thickness taken at the base of the sternum. Bold, seals examined histologically ($n = 7$).

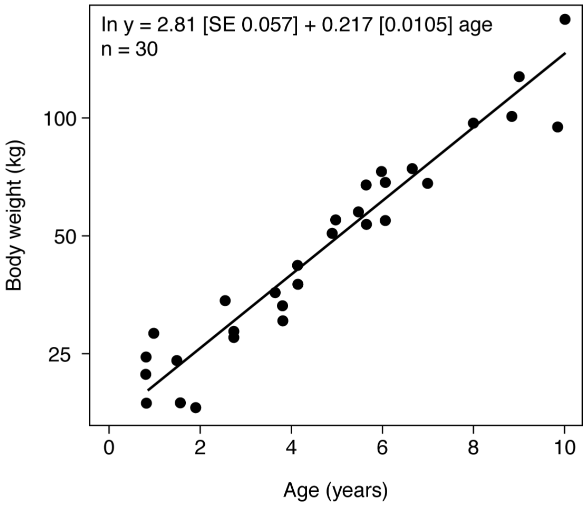


Fig. 2.1 The relationship between log body weight (kg) and age (y) in the male Cape fur seal.

r = the factor by which body weight is multiplied for each additional year of age, and t = time in y. The equation may equivalently be written:

$$\log(\text{weight}) = \log(w_o) + t \log r$$
$$\text{weight} = a_o + ct$$

where $a_o = \log(w_o)$ and $c = \log r$. The same equation was used to determine the relationship between organ weight and age (y).

Histology

Sections of the heart, lung, liver, spleen, stomach, intestine and kidneys were fixed in 10% phosphate buffered formalin for a minimum of 24 h before being stored in 70% alcohol prior to routine processing for histological analysis (Drury & Wallington, 1967). Sections of wax embedded tissues (5–10 µm) were stained with haematoxylin and eosin. Tissues showed variable degrees of autolysis. Where appropriate, this has been mentioned in the results for specific organs.

Table 2.2 *Mean by age class of relative weights of the heart, lung, liver, spleen, stomach, intestine and kidneys in the male Cape fur seal*

Age (y)	No.[a]	Body weight[b] (kg)	Heart	Lung	Liver	Spleen	Stomach	Intestine	Kidneys
1	4	23	0.5	2.1 (3)	2.6	0.1	1.0	3.6 (3)	0.6
2	3	20	0.6	2.7	3.8	0.2	1.6	5.0	1.0
3	3	30	0.5	2.3	3.3	0.2	1.4	5.2	0.8
4	5	36	0.5	2.8	3.6	0.2	1.3	4.8	0.8
5	2	53	0.5	2.6	4.1	0.2	1.7	5.3	0.8
6	6	62	0.6	2.7 (5)	4.5	0.3	1.5	4.6 (5)	0.8
7	2	71	0.6	2.0 (1)	4.3	0.2	1.6	4.6 (1)	0.8
8	1	97	0.7	–	4.4	0.2	1.6	–	0.8
9	2	115	0.6	2.7 (1)	3.8	0.3	1.3	3.5 (1)	0.8
10	2	137	0.6	2.5 (1)	4.3	0.4 (1)	1.4	3.8 (1)	0.8
Mean			**0.5**	**2.5**	**3.8**	**0.2**	**1.4**	**4.5**	**0.8**
Total	**30**	**30**	**30**	**24**	**30**	**29**	**30**	**24**	**30**

Organ sample size is given in brackets where this does not equal total sample size.

[a] Total number of seals.

[b] Mean body weight.

Age determination

The age of animals was estimated from counts of incremental lines observed in the dentine of tooth sections. Upper canines were sectioned longitudinally using a circular diamond saw. Sections were ground down to 280–320 µm, dehydrated, embedded in resin and viewed under a stereomicroscope in polarised light (Oosthuizen, 1997). Each section was counted 5 times by an individual reader and ages were rounded off to the nearest birth date. The median date of birth was assumed to be 1 December (Shaughnessy & Best, unpublished report). For the purpose of this study the following age classes were used: juvenile (< 1 y and 6 mo); 2-y-old; subadult (3–7 y); adult (≥ 8 y of age).

RESULTS

Details of the 31 male specimens are presented in Table 2.1. They ranged from 6 mo to 10 y of age. Body lengths varied between 90 and 189 cm, and body weights between 16 and 179 kg. All animals were in good physical condition as inferred from blubber thickness, i.e., blubber thickness ranged from 2.0–2.7 cm in juveniles and up to 4.0 cm in adults.

Body weight and age

The relationship between body weight and age (y) is presented in Fig. 2.1. The fitted line represents the exponential growth equation, weight = $w_o r^t$, with body weight on the log transformed vertical axis and t (time in y) on the horizontal axis. For the range of ages represented in this study, data are consistent with a constant relative increase of 23% per y until at least 9–10 y of age.

Organ size

Mean body weights, and mean relative organ weights, by age class are presented in Table 2.2.

Organ growth

The relationship between organ weight, body weight and age is presented in Fig. 2.2*a*, *b*. In Fig. 2.2*a* the fitted line represents the allometric equation, $y = ax^b$, with organ weight on the log transformed vertical axis, and body weight on the log transformed horizontal axis. When data on seals of all age classes are considered, exponents b (the slope of the line) for the lungs, stomach, intestine and kidneys were not significantly different from 1, suggesting that these organs increased in weight in proportion to the body weight. However, the heart, liver and spleen had exponents $b > 1$, suggesting that these organs increased at a faster rate than the body (Table 2.3).

In Fig. 2.2*b* the fitted line represents the exponential growth equation, weight = $w_o r^t$, with organ weight on the log transformed vertical axis and t (time in y) on the horizontal axis. Organ weight increased at a rate of between 25% and 33% per year until at least 9–10 y of age (Table 2.3).

Gross and microscopic anatomy

Heart

The heart was positioned obliquely within the thoracic cavity, slightly to the left, between the 3rd and the 7th rib (Fig. 2.3). The heart was flat and broad, with a slight bifurcation at its apex (Fig. 2.4). Partially covered by the surrounding lungs, it was enclosed in a pericardium and attached at the apex to the diaphragm. It possessed the typical mammalian

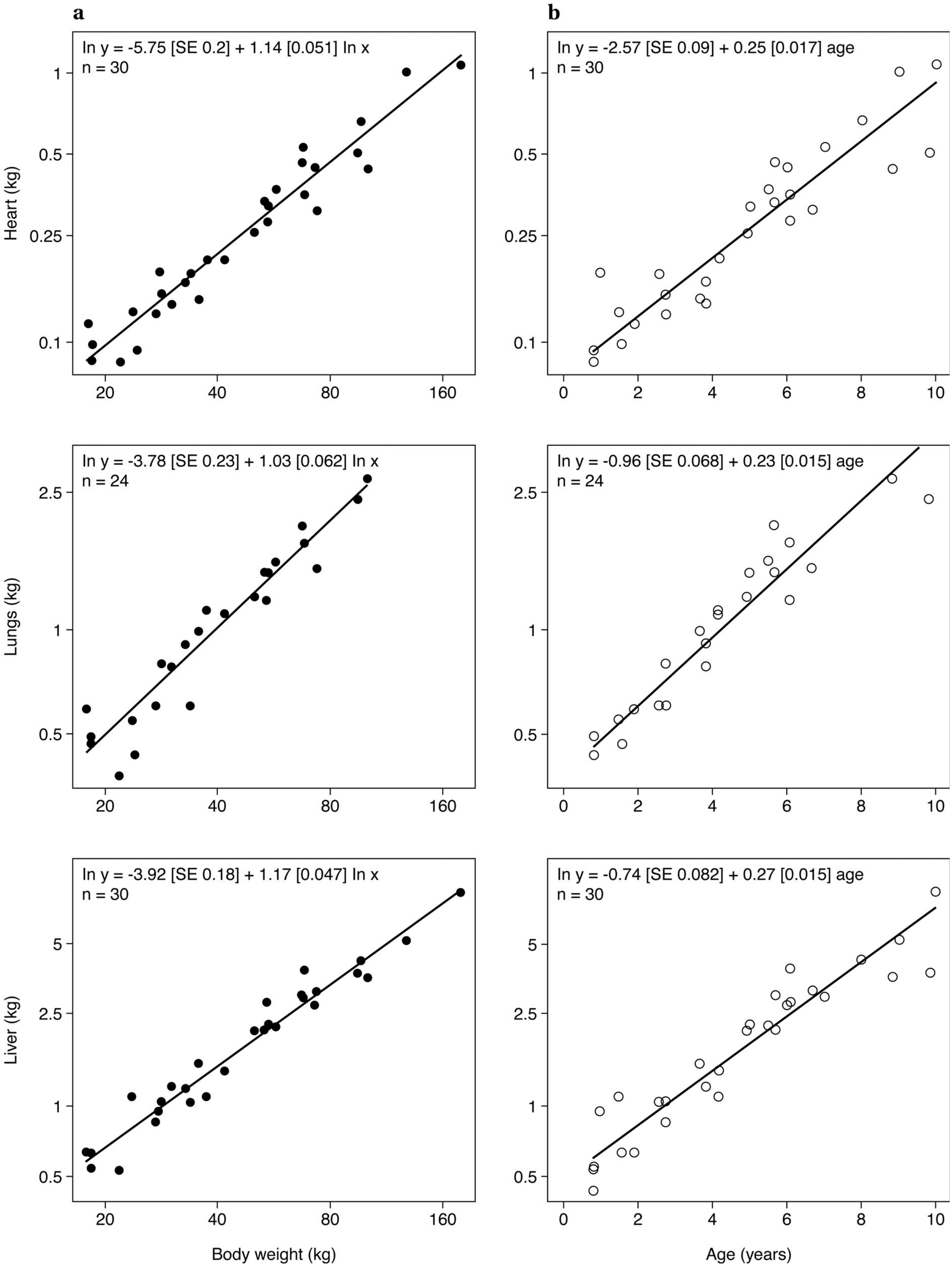
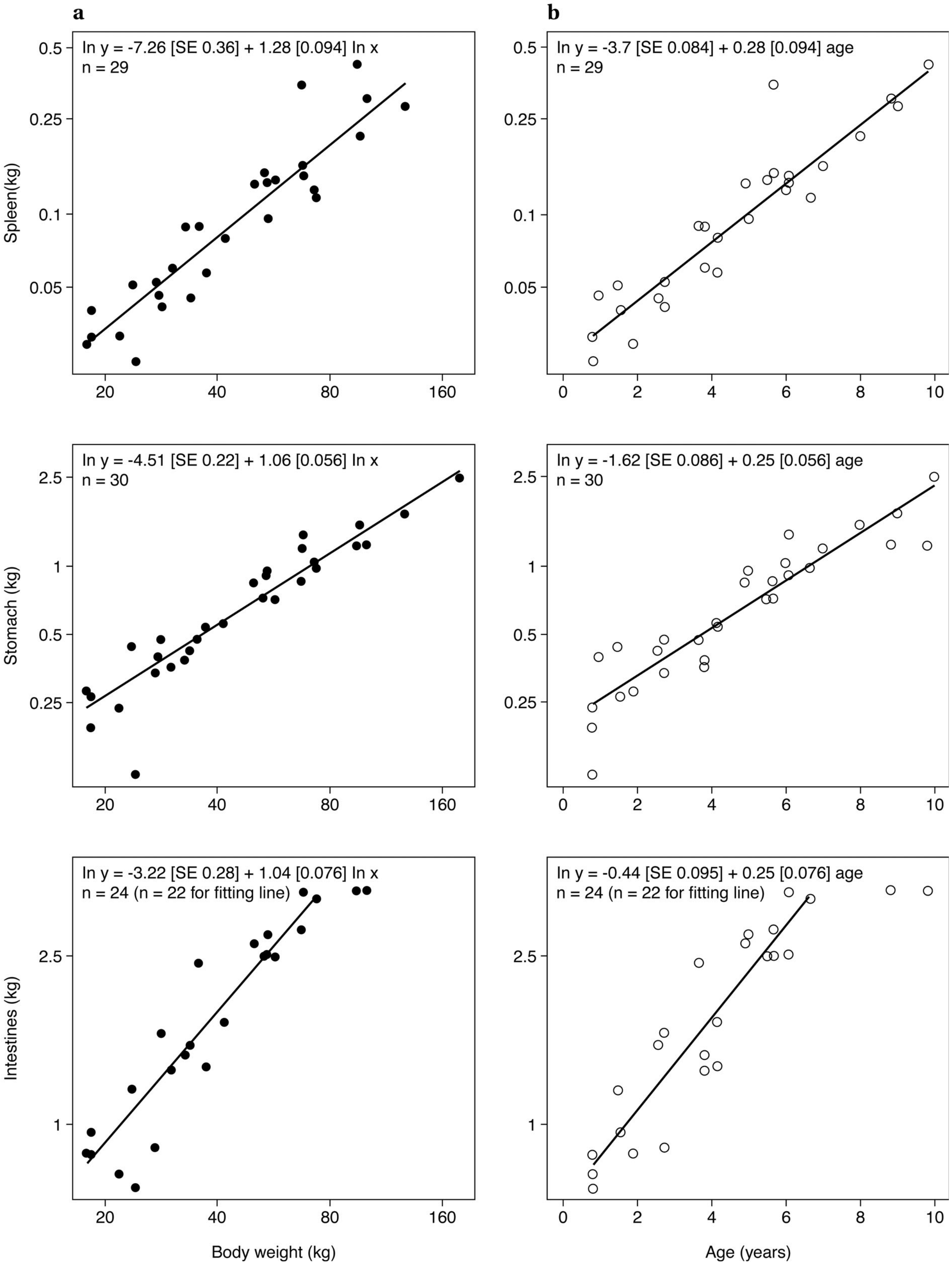


Fig. 2.2 For legend see page 25.



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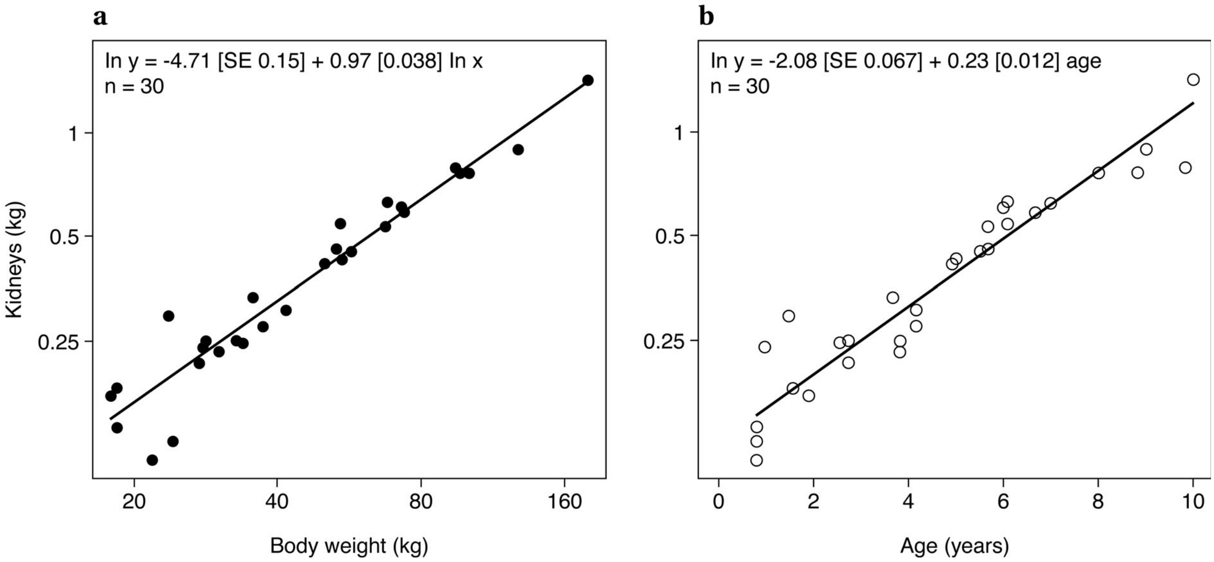

Fig. 2.2 The relationship between (*a*) log organ weight and log body weight ($y = ax^b$), and (*b*) log organ weight and age (weight = $w_o r^t$) in the male Cape fur seal.

Organ sample size: heart, 30; lung, 24; liver, 30; spleen, 29; stomach, 30; intestine, 24; kidneys, 30.

Exponent b, slope of the regression line; S.E. [b], standard error of *b*.

Note: the unusually large spleen found in a 6 y-old animal (AP3589), which the robust fitting routine has effectively excluded in fitting the line. For intestines, where exponential increase appears to have ceased by *c*. 7 y, we used only seals less than 7 y in fitting the line.

Table 2.3 ***Organ weight in relation to body weight and age in the male Cape fur seal***

	Exponent *b*[a]	**S.E. [*b*]**	**D.F.**	***P***	***c*[b]**	**S.E. [*c*]**	**increase per y (%)**
Whole body	–	–	28	–	0.22	0.011	23
Heart	1.14	0.05	28	0.01	0.25	0.017	28
Lung	1.03	0.06	22	NS	0.23	0.015	26
Liver	1.17	0.05	28	0.001	0.27	0.015	31
Spleen	1.28	0.09	27	0.005	0.28	0.016	33
Stomach	1.06	0.06	28	NS	0.25	0.016	28
Intestine	1.04	0.08	20	NS	0.25	0.023	29
Kidneys	0.97	0.04	28	NS	0.23	0.012	25

Estimation of b and c values for the allometric equation $y = ax^b$, and the exponential growth equation weight = $w_o r^t$.

[a] *b* is the exponent in $y = ax^b$.

[b] *c* is log *r*, where *r* is the factor by which the organ weight is multiplied for each additional year of age in the exponential growth equation, weight = $w_o r^t$.

NS, not significant at the 0.05 level for a test that $b = 1$.

arrangement of 4 chambers separated by aortic, pulmonary, left and right atrioventricular valves (Evans, 1993). The arrangement of the arteries was most similar to that found in *Neophoca* spp. (King, 1983. p. 179). The ascending aorta enlarged at the level of the brachiocephalic artery to form an aortic bulb.

Samples of left and right ventricles, left atrium, aortic arch, pulmonary trunk, pulmonary artery and aortic valve from 3 seals; right atrium from 2 seals, and right pulmonary valve from 1 seal were examined histologically. All animals were adult.

The cardiac tissue had usual mammalian features. The epicardium consisted of mesothelium overlying prominent connective tissue and was associated with variable adipose tissue. Connective tissue trabeculae containing blood vessels penetrated the myocardium. The endocardium was thicker in the ventral left ventricle than at the other sites examined but overall the endothelium did not appear unusually thick. The appearance of the myocardial cells was unremarkable and Purkinje cells were difficult to distinguish morphologically from other myocardial cells.

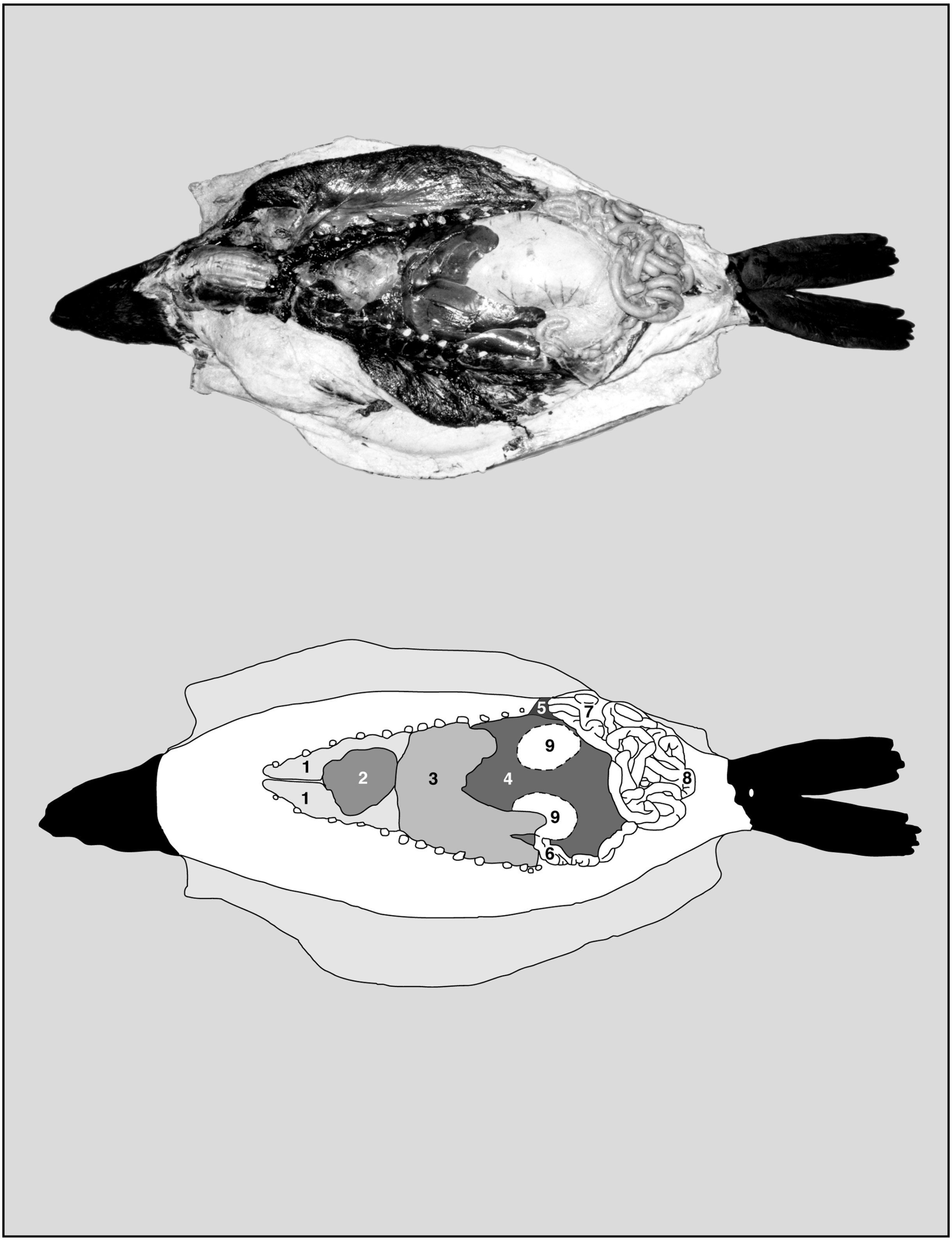

Fig. 2.3 Orientation of the major organs within the thoracic cavity of a 9 y-old (adult) Cape fur seal, ventral aspect. 1, lung; 2, heart; 3, liver; 4, stomach; 5, spleen; 6, duodenum; 7, small intestine; 8, large intestine; 9, kidneys (dorsal to the stomach).

The pulmonary and aortic valves consisted of dense connective tissue with some apparent elastic fibres, and had endocardium on both sides. The aortic valve had prominent layers of probable elastic fibres at its base. The aorta was a typical thick-walled, elastic artery with a thick adventitia. The pulmonary artery was a muscular artery with prominent endothelial cells.

Lungs

The trachea and bronchi of the mature Cape fur seal (e.g., AP4992) were supported dorsoventrally by incomplete cartilaginous rings. Within this distinct dorsal gap, the oesophagus was attached within connective tissue. Bifurcation of the trachea into 2 main stem bronchi occurred *c.* 13 cm caudal to the larynx. The main stem bronchi ran parallel until they diverged at a 2nd bifurcation *c.* 30 cm caudal to the larynx.

The distinct dorsal gap observed in the adult bronchi was absent in the juvenile (e.g., AP5162). Instead, the cartilaginous rings overlapped dorsally. The bronchi entered the lungs at the same level as the pulmonary vein. Bifurcation occurred *c.* 10 cm caudal to the larynx.

The position of the lungs and heart within the thorax is illustrated in Fig. 2.3. The lungs were multilobed with deep fissures between each lobe (Figs. 2.5, 2.6). The right lung consisted of cranial, middle, caudal and accessory lobes. The right cranial lobe was broadly triangular, whereas the right middle lobe was smaller and elongated. The right caudal lobe was triangular, and had a cone-shaped, partially ridged accessory lobe extending from its ventral surface. The middle and caudal lobes were attached to one another along 10% of their borders, while 1/3rd of the accessory lobe was attached to the caudal lobe.

The left lung consisted of a divided cranial lobe and an undivided caudal lobe. The left caudal lobe was triangular in shape. The left cranial lobe consisted of 2 distinct divisions that were attached to one another along *c.* 40% of their borders by connective tissue.

Lung samples taken from multiple sites were obtained from 2 adult seals and examined in more detail histologically. One seal had a group of nematodes present in the lung and limited areas of focal pneumonia. These areas were not included in the following description. The lungs of both seals showed congestion, oedema and collapse of smaller airways, consistent with lung compression. Pulmonary oedema, although a nonspecific change, may have been due to drowning (Cooke, 1993).

The pleura was thick and consisted of 3 layers (Fig. 2.7). Beneath the outer mesothelial layer was a thin layer of probable elastic tissue, beneath which was a thick layer of loose connective tissue containing blood vessels, lymphatic vessels and some nerves. Fibrous septa extending from the pleura were very prominent.

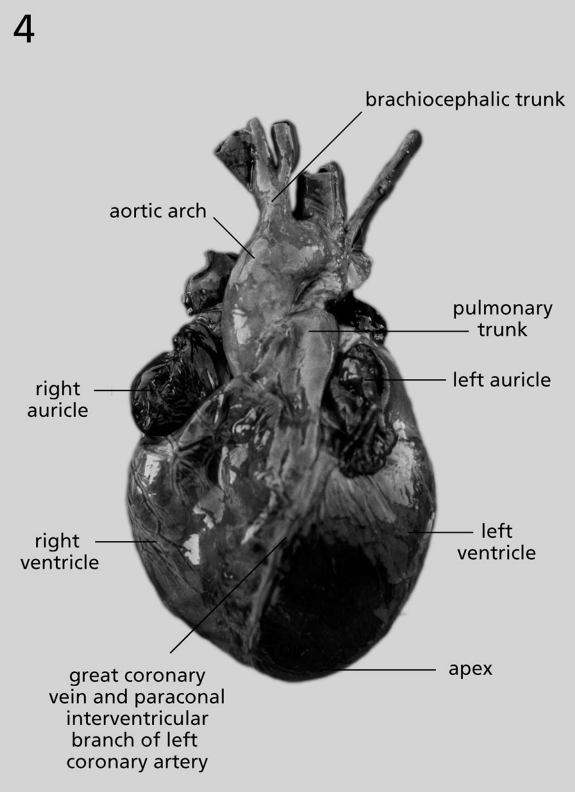

Fig. 2.4 Heart of a Cape fur seal, dorsoventral.

Larger airways, including the primary bronchus, had folded epithelium, presumably due to airway collapse. The pseudostratified columnar epithelium was underlain by a prominent layer of acellular, dense connective tissue. Beneath this layer was vascular connective tissue surrounded by an incomplete layer of smooth muscle. External to this muscular tissue was connective tissue interspersed with mucous glands and blood vessels. Cartilage plates surrounded this connective tissue layer and external to the cartilage were some mucous glands and a surrounding thin layer of connective tissue. Mucous glands were absent from smaller airways. Goblet cells were numerous in the epithelium, especially in larger airways. Histological features of a large intrapulmonary airway are shown in Fig. 2.8.

The height of the epithelium was decreased in smaller airways, eventually becoming low columnar to cuboidal, and the surrounding layers were less well developed. Cartilage was present in even very small airways, including airways with simple cuboidal epithelium from which alveoli originated. A complete smooth muscle layer was present in smaller airways, and isolated smooth muscle bundles were observed in alveolar septa (Fig. 2.9). Lymphoid aggregates, scattered lymphocytes and plasma cells were commonly present in the lamina propria and submucosa of airways.

Examination of a single section of trachea revealed histological features similar to those of large intrapulmonary airways. Adipose tissue, muscle and blood vessels were found external to the tracheal cartilage.

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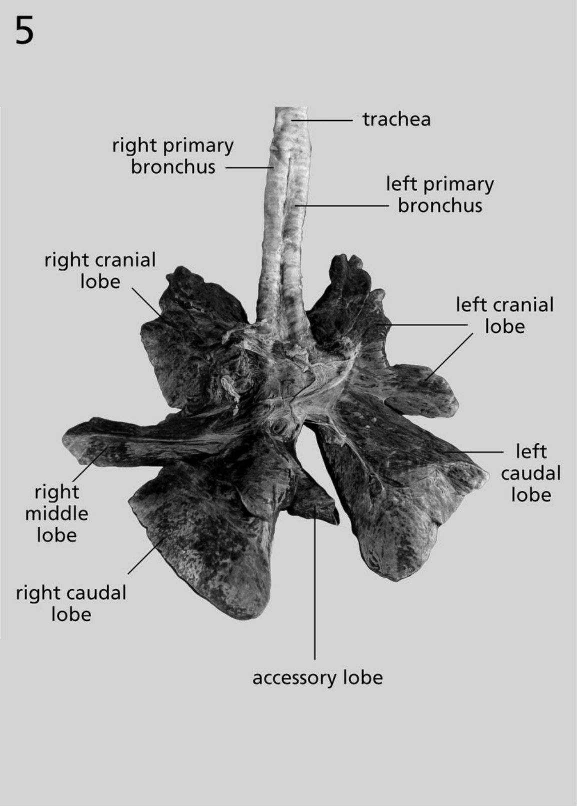

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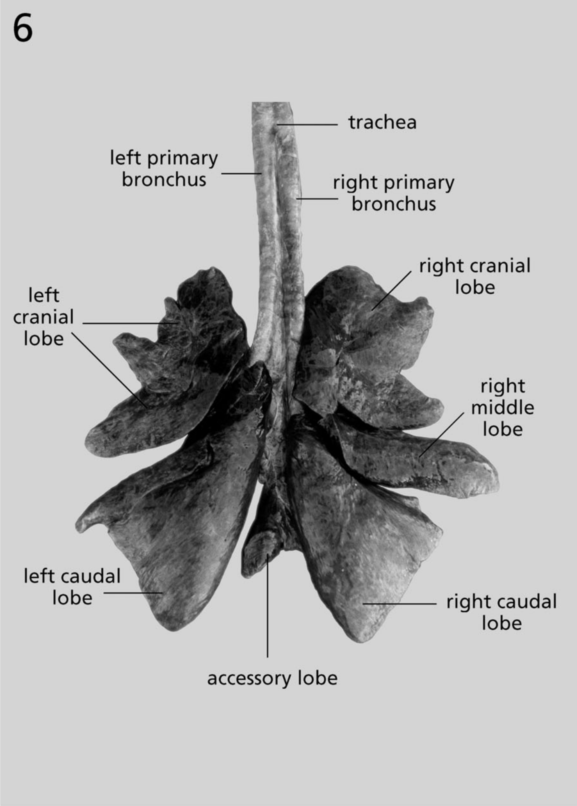

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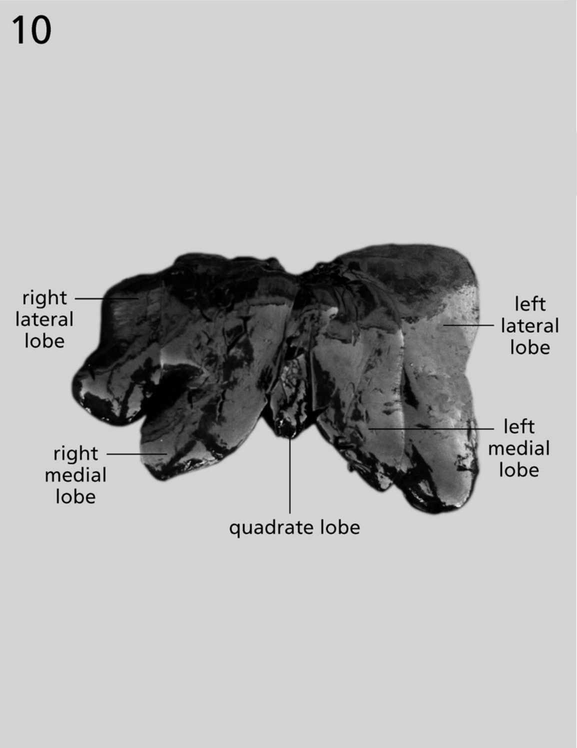

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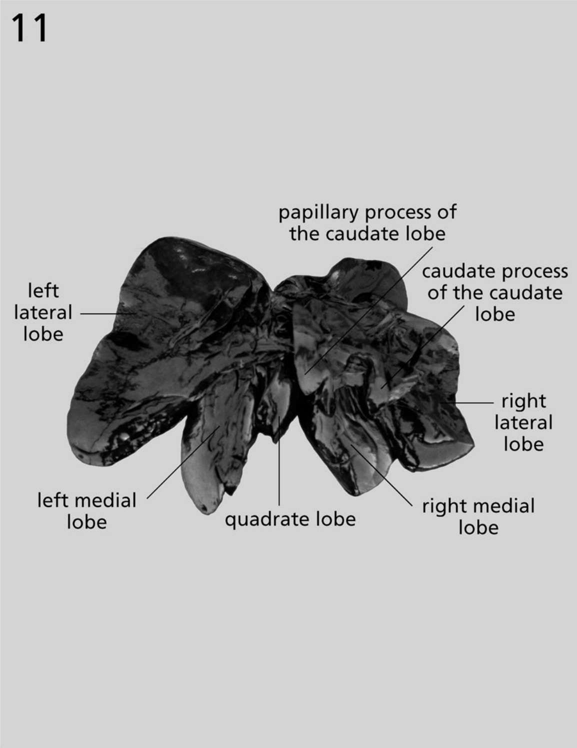
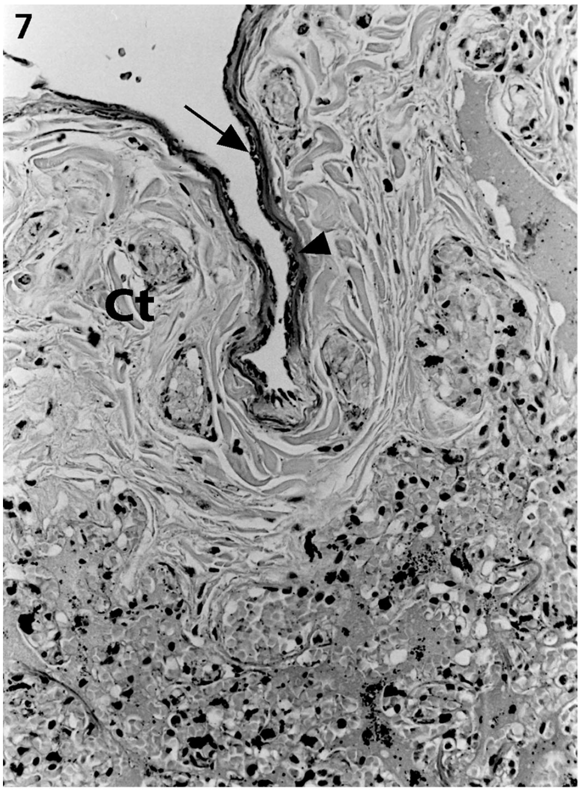
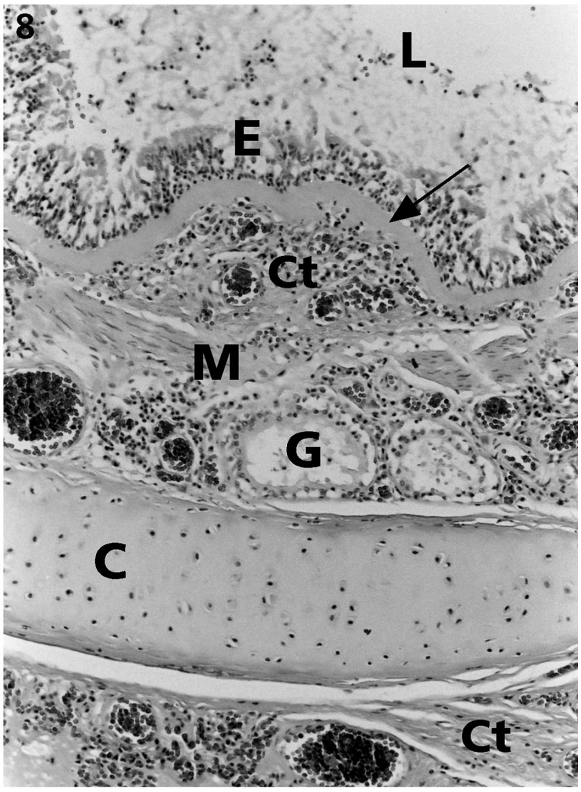
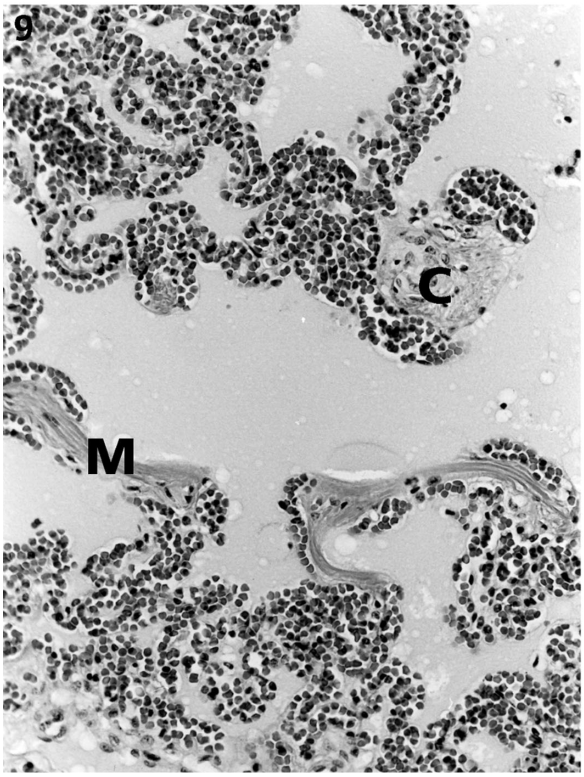


Fig. 2.5 Lung of a Cape fur seal, ventral aspect.
Fig. 2.6 Lung of a Cape fur seal, dorsal aspect.
Fig. 2.10 Liver of a Cape fur seal, diaphragmatic aspect.
Fig. 2.11 Liver of a Cape fur seal, visceral aspect.







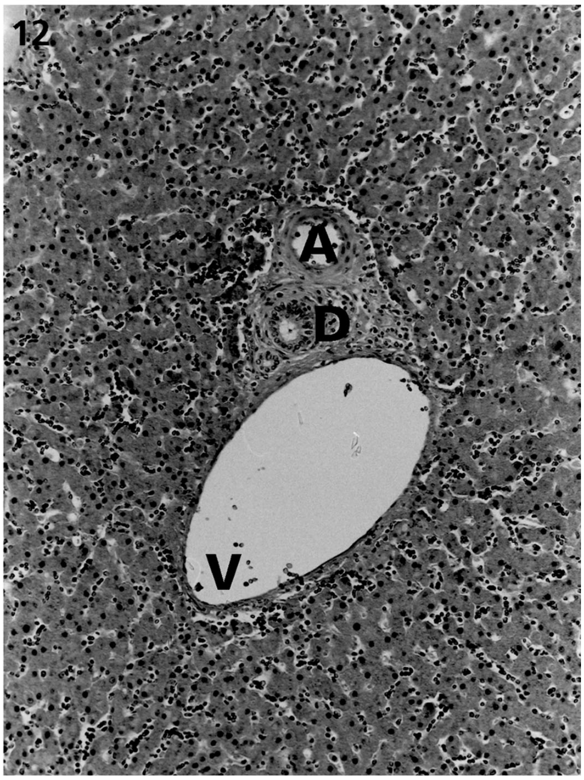
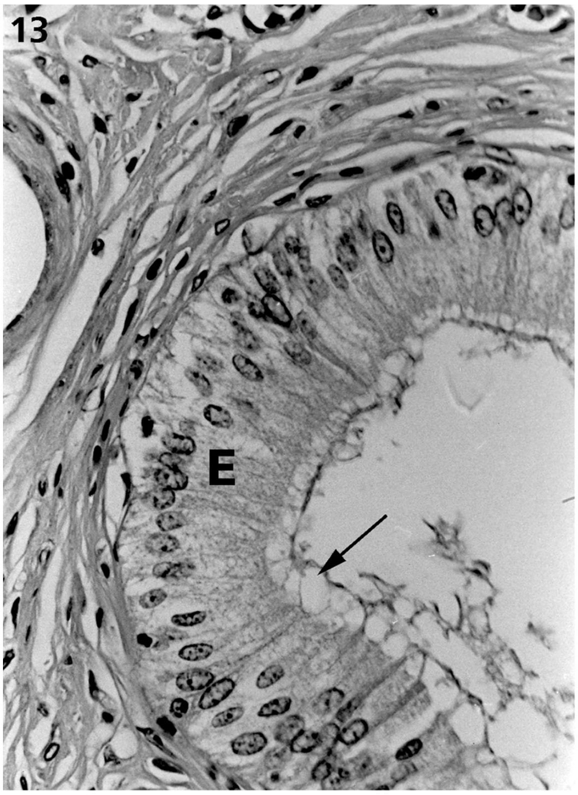


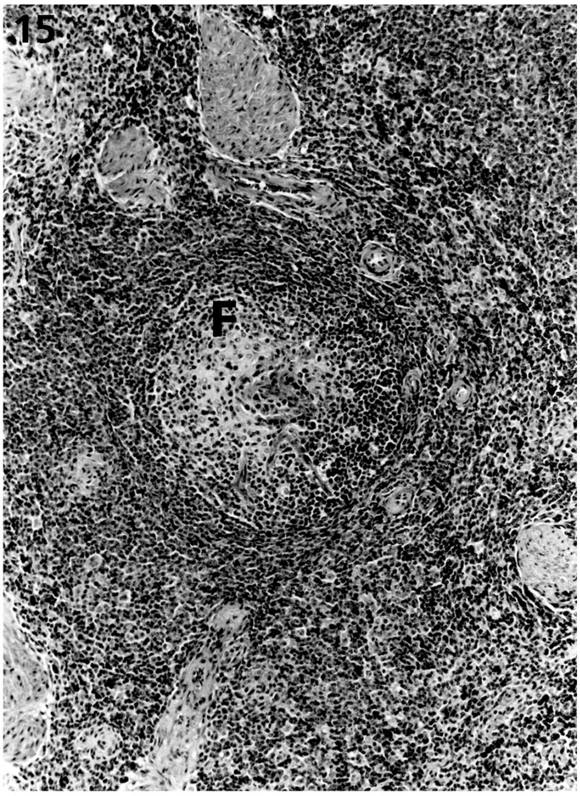
Fig. 2.7 Pulmonary pleura of a Cape fur seal demonstrating the presence of an outer mesothelial layer (arrow), an underlying layer of probable elastic tissue (arrow head) and a deep layer of loose connective tissue (Ct). H & E, × 180.

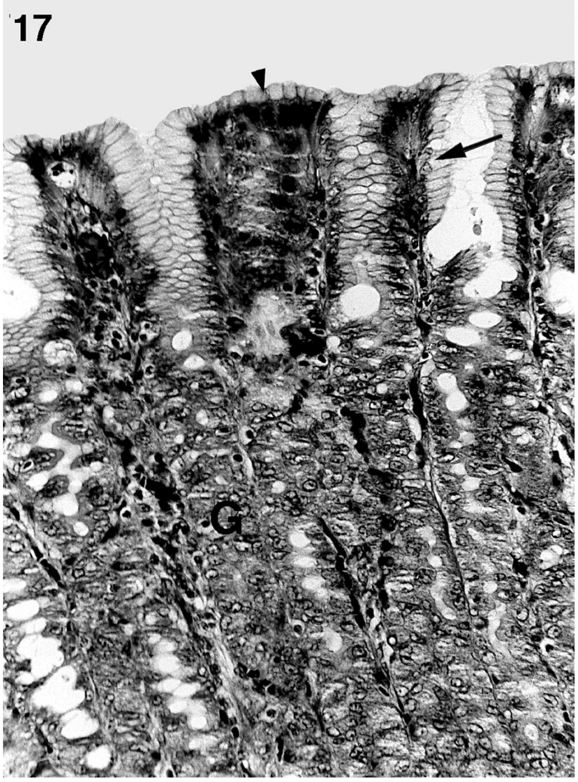
Fig. 2.8 Components of the wall of a large intrapulmonary airway of a Cape fur seal. The epithelium (E) is underlain by a layer of acellular, dense connective tissue (arrow) that overlies vascular loose connective tissue (Ct). Deep to this connective tissue, an incomplete layer of smooth muscle (M) overlies vascular connective tissue that contains mucous glands (G). Cartilage plates (C) surrounded by loose connective tissue (Ct) comprise the outermost components of the wall. Epithelial disruption and the presence of debris in the lumen (L) may be due to post mortem tissue deterioration or could have resulted from drowning. H & E, × 35.

Fig. 2.9 Lungs of a Cape fur seal demonstrating the presence of cartilage (C) in the wall of a very small airway and smooth muscle (M) in the alveolar septa. Congestion and oedema are apparent. H & E, × 180.

Fig. 2.12 Portal area of the liver of a Cape fur seal demonstrating the presence of a branch of the hepatic portal vein (V) and hepatic artery (A) in company with a bile ductule (D). A smooth muscle sphincter surrounding the vessels is not apparent. H & E, × 90.







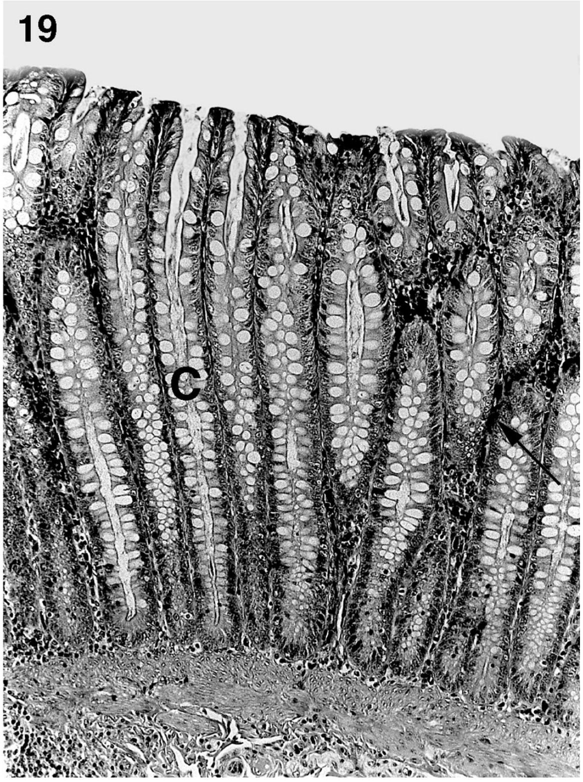


Fig. 2.13 Large intrahepatic bile duct of a Cape fur seal demonstrating tall columnar epithelium (E) with apical clear spaces probably corresponding to mucus removed in processing (arrow). H & E, × 350.

Fig. 2.15 Spleen of a Cape fur seal demonstrating a lymphoid follicle (F) with prominent germinal centre. H & E, × 90.

Fig. 2.17 Body of the stomach of a Cape fur seal demonstrating mucous surface cells (arrowhead), mucous neck cells (arrow) and the proximal bodies of fundic glands (G). H & E, × 180.

Fig. 2.19 Colon of a Cape fur seal demonstrating the presence of numerous straight tubular crypts (C) with abundant goblet cells. Lymphoid cells (arrow) are evident in the lamina propria. H & E, × 90.

Liver

The liver was located primarily within the right side of the abdominal cavity and extended craniocaudally from the 6th sternal to the 3rd, and final, asternal rib (Fig. 2.3). The liver had 6 distinct lobes, separated by deep natural fissures (Fig. 2.10, 2.11). From the ventral aspect, the left lateral (16.9 × 11.7 cm), left medial (21.2 × 8.9 cm), right medial (21.2 × 13.0 cm) and right lateral lobes (17.2 × 8.5 cm) could be readily distinguished. The quadrate lobe (13.2 × 7.0 cm) was located between left and right medial lobes. On the visceral aspect of the right lateral lobe was the caudate lobe, which had a caudate process (6.9 × 6.5 cm) and a papillary process (4.8 × 6.5 cm). Measurements were taken from PEM2198 (juvenile).

The piriform gall bladder was *c.* 6.5 cm long and 3.0 cm wide at its greatest diameter. It was located at the ventral surface of the right medial lobe, to the right of the ligamentum teres. The bile duct entered the proximal duodenum at the same level as the pancreatic duct.

Liver samples from 2 adult seals were examined in more detail histologically. Both livers had widespread areas of focal necrosis and leukocyte infiltration, and 1 had microabscessation. In 1 seal, hepatocellular vacuolation was common and in the other, perivascular connective tissue and lymphoid infiltration were widespread.

On examining relatively normal areas, the liver was found to have usual mammalian features. It was surrounded by a connective tissue capsule and hepatocytes were arranged in laminae of single sheets of cells. Portal areas were readily discernible but no obvious smooth muscle sphincter around vessels was seen (Fig. 2.12). Interlobular connective tissue was not prominent. Small bile ducts had cuboidal epithelium while ducts of larger diameter had more columnar epithelium, with probable apical mucus (Fig. 2.13). Gold brown pigment granules were present within many hepatocytes of 1 seal but were not obvious in the liver of the other animal. Kupffer cells were not prominent.

Spleen

The spleen was loosely attached to the greater curvature of the stomach by the gastrosplenic ligament (Fig. 2.3). This flat, elongated rectangular organ was *c.* 33 cm long and 8 cm wide at the broadest part in adults ($n = 3$ seals). The cranial extremity was generally rounded and the caudal extremity tapered (Fig. 2.14). Dark red pigmentation could be seen scattered throughout the spleen. No accessory spleens were observed.

Splenic tissue from 5 adult seals was examined histologically. Features were typically mammalian. The capsule was thick and trabeculae were very prominent. Large trabeculae contained arteries, veins and nerves. The parenchyma consisted of white and red pulp but the degree of development of lymphoid tissue was variable among individuals. Lymphoid tissue consisted of periarteriolar lymphoid sheaths (PALS) and follicles but follicles generally predominated over PALS (Fig. 2.15). Most follicles had germinal centres, some of which showed hyaline deposits. Plasma cells were very numerous throughout the red and white pulp and occasional plasma cells were binucleate. Sheathed capillaries were not prominent. Gold brown pigment granules were present in macrophages scattered throughout the spleen. No megakaryocytes or haematopoietic islands were evident in the red pulp.

Stomach

The stomach was single chambered and J-shaped. The cardia and fundus were not well developed, therefore the region between the end of the oesophagus and the angular notch will be referred to as the body. The distal 3rd of the stomach, the pyloric portion, was directed cranially from the angular notch and narrowed into a small ostium (Fig. 2.16). The pyloric sphincter was well developed. Rugae lined the body of the stomach, whereas the pyloric portion was comparatively smooth.

The body of the stomach was located within the left side of the abdominal cavity, and the pyloric portion within the right (Fig. 2.3). When distended, the body of the stomach extended caudoventrally as far as the pelvis. The stomach was intimately associated with the liver, spleen and intestine.

Tissue samples taken from the body and pyloric regions of the stomach of 3 seals were examined histologically. Tissues from 2 animals showed signs of autolysis. Therefore, description of the epithelium and lamina propria of the surface mucosa was not possible in these animals. Neutrophilic debris was present within some of the pyloric glands of the 3rd seal. This animal had prominent diffuse and follicular lymphoid tissue in the lamina propria of both regions of the stomach and mild neutrophilic infiltration of the lamina propria of the pyloric region. Least affected areas were used for histological description.

The surface epithelium was simple columnar and consisted of cells with the typical appearance of gastric surface mucous cells. Gland neck cells were also columnar mucous cells (Fig. 2.17). The deeper parts of the glands in the body region had the typical appearance of fundic glands. They were simple, branched tubular glands with most epithelial cells consistent in appearance with chief cells and parietal cells. The latter were numerous. In the pyloric region, mucous glands were present. They were simple, branched tubular glands separated by a small amount of connective tissue. Primary lymphoid follicles were present in the deep lamina propria, particularly in the pyloric region, sometimes extending between layers of the muscularis mucosae. Scattered lymphoid cells were present in the connective tissue between glands. The muscularis mucosae was prominent with multiple layers. The submucosa consisted of loose vascular connective tissue which contained some bundles of nerve cells. Lymphocytes, plasma cells and neutrophils were

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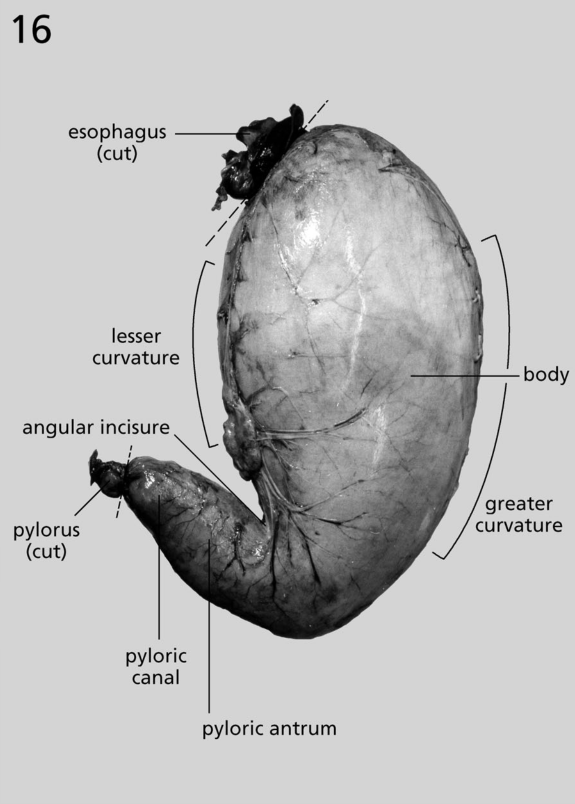

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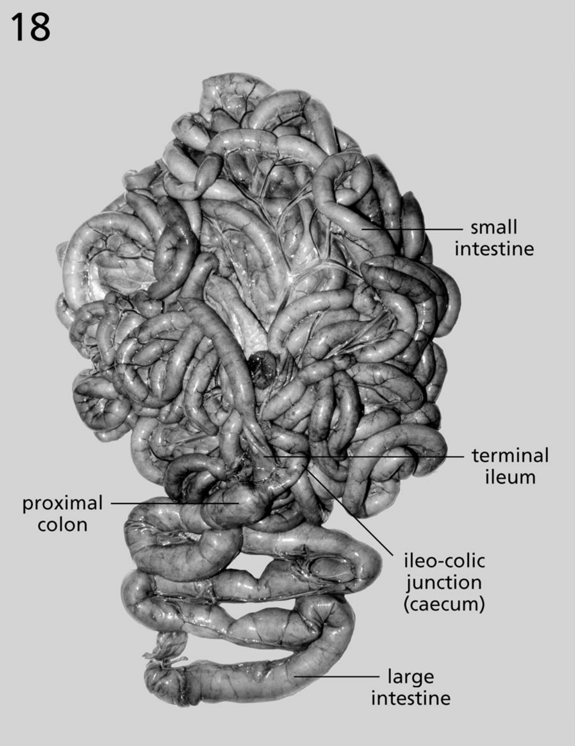

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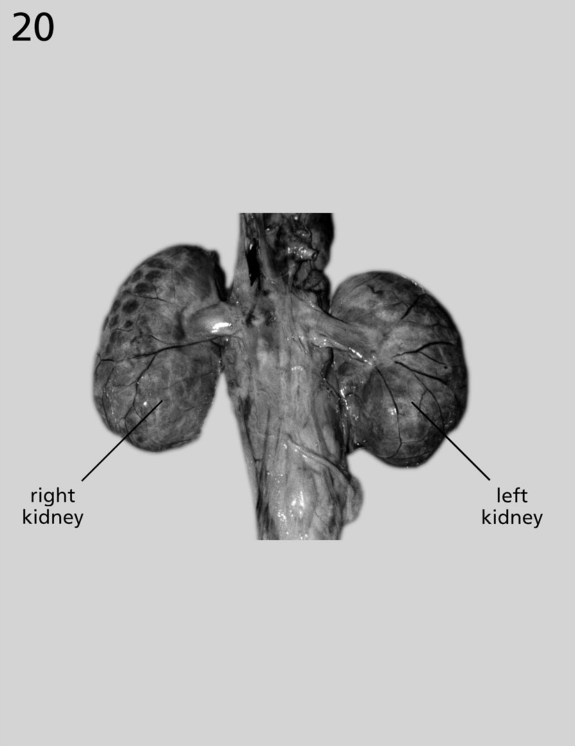
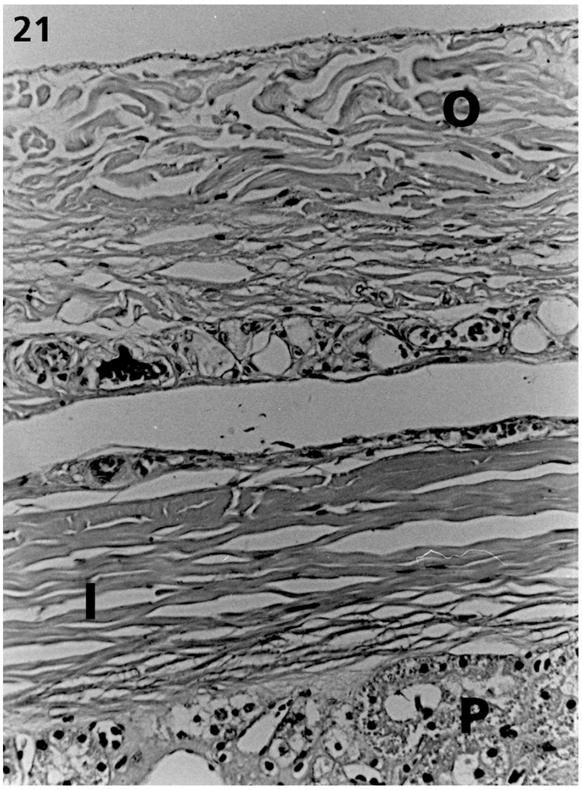


Fig. 2.14 Spleen of a Cape fur seal, parietal aspect.

Fig. 2.16 Stomach of a Cape fur seal.

Fig. 2.18 Intestine of a Cape fur seal. Note the small diverticulum at the ileo-colic junction.

Fig. 2.20 Kidneys of a Cape fur seal, ventral aspect.



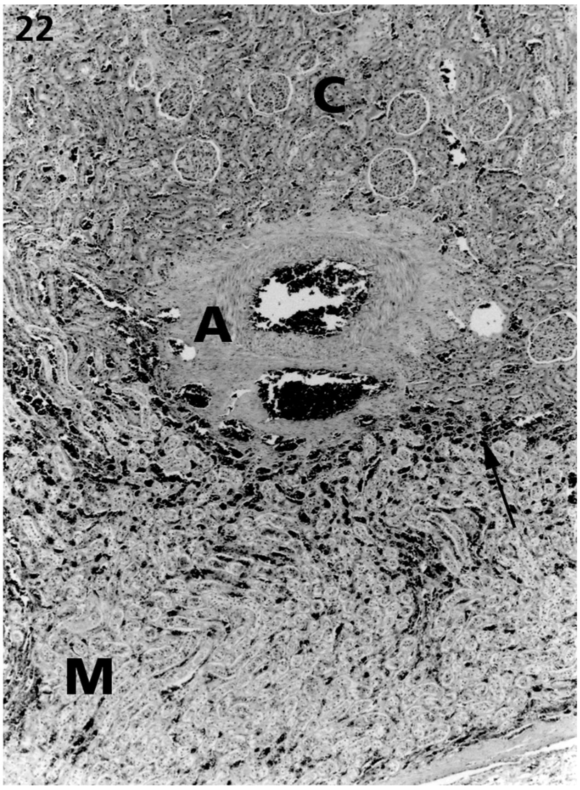


Fig. 2.21 Renal capsule of a Cape fur seal demonstrating an outer layer (O) separated from an inner layer (I) that is adherent to the parenchyma (P). H & E, × 180.

Fig. 2.22 Kidney of a Cape fur seal demonstrating the presence of muscular arteries (A) at the corticomedullary junction (arrow) but no apparent smooth muscle bundles representing a sporta peri medullaris musculosa. C, cortex; M, medulla. H & E, × 35.

variably present. The tunica muscularis consisted of 2 to 3 layers which were not always readily distinguishable. The innermost layer had an oblique to circular orientation and the outermost and middle layers had an oblique to longitudinal orientation. Loose connective tissue containing vessels and bundles of nerve cells was present between the layers of the tunica muscularis.

Small and large intestine

The duodenum began at the pylorus, immediately formed a U-shaped loop to the left, passed across the ventral surface of the pylorus, and coursed caudally along the right lateral wall of the abdomen (Fig. 2.3). The duodenojejunal flexure was not distinct, thus it was difficult to distinguish grossly the duodenum from the jejunum. The jejunum formed extensive loops that were supported by well developed, fan-shaped mesentery. The ileum, which could not be distinguished grossly from the jejunum, terminated at a much reduced caecum which comprised a small diverticulum, 4.5–6.0 cm long, at the ileo-colic junction (Fig. 2.18). The large intestine was comparatively short and its lumenal surface was smooth.

The small intestine was narrow and long. For example, in 1 adult seal, the dimensions were 265 cm in length and 1.7 cm in width. The large intestine was slightly wider in diameter with few flexures. Dimensions were 120 cm in length, excluding the caecum and anal cavity, and 3.0 cm in width. The total length of the adult intestinal tract was *c.* 28 m ($n = 4$) and ranged from 25 to 32 m, 16 times the length of the body. Juvenile intestinal length was 13 m, 12 to 14 times the length of the body ($n = 2$).

Tissue samples from the jejunum and colon of 1 seal were examined histologically. The lamina propria of both regions of the intestine was moderately to heavily infiltrated with lymphoid cells and neutrophils and some crypts contained neutrophils (crypt abscesses). There were some associated areas of fibrosis in the small intestine. The least affected areas were used for histological examination.

The small intestinal villi were very long, slender and irregular in outline. The apical tips of some villi appeared to be fused. The epithelium was simple, consisting predominantly of columnar enterocytes, between which were lesser numbers of goblet cells and lymphocytes. Tubular crypts penetrated the lamina propria between the villi. The lamina proprial connective tissue contained vessels, lymphoid cells and some neutrophils and eosinophils. Smooth muscle was also present in the villous cores. The muscularis mucosae was prominent and appeared to consist of 2 ill defined layers. The submucosa consisted of vascular loose connective tissue in which bundles of nerve cells could be seen. The tunica muscularis consisted of a thicker inner circular and a thinner outer longitudinal layer, between which bundles of nerve cells were evident.

The large intestine was nonvillous and had numerous straight tubular crypts penetrating the mucosa. Goblet cells were very numerous, especially in the crypts (Fig. 2.19). The surface epithelium was simple columnar. Between the crypts was sparse connective tissue with lymphoid cells and fewer numbers of neutrophils and eosinophils. The muscularis mucosae was prominent and had an inner circular layer and an outer longitudinal layer. The submucosa consisted of loose connective tissue containing bundles of nerve cells and primary lymphoid follicles. The tunica muscularis was similar in arrangement to that of the small intestine.

Kidneys

The kidneys were situated in the sublumbar region, 1 each side of the vertebral column, extending from the 2nd asternal rib to just beyond the last rib (Fig. 2.3). They were loosely attached to the abdominal muscle by connective tissue. The left kidney was slightly more caudal than the right. Each kidney was composed of numerous reniculi separated by shallow furrows and was covered by a fibrous capsule (Fig. 2.20). The average dimensions of the adult kidney were length (13.6 cm), width (7.9 cm) and height (5.9 cm) ($n = 3$). The right and left kidneys were essentially the same size and shape; a test for statistical significance of the quadratic term for kidney size having $P = 0.2$ (D.F. = 21).

Samples of renal tissue from 3 adult seals were examined in more detail histologically. The kidneys were renicular. Each single medullary papilla had an obvious inner and outer part and was enclosed by a calyx. The capsule was thick and consisted of a loose outer layer containing variable fat and vessels, and a more tightly adherent inner layer (Fig. 2.21). Extracapsular fat was present in 2 seals. Beneath the capsule, within the periphery of the cortical tissue, were numerous veins. Muscular arteries embedded in connective tissue were present at the corticomedullary junction (Fig. 2.22). While their walls appeared to contain generous amounts of smooth muscle, there were no distinct muscle bundles discernible at the corticomedullary junction. The distinction between adjacent reniculi was usually marked by the presence of arteries and veins but not connective tissue septa. The glomeruli and tubules had the usual mammalian arrangement. The submucosa of the base of the calyx consisted of ample vascular connective tissue. The calyx was lined by transitional epithelium which became 1 to 2 cells thick as it was reflected over the papilla. Branches of the ureter were lined by transitional epithelium and were surrounded by thick connective tissue.

Lymphoid infiltration of the submucosa and/or epithelium of the calyx was seen in the 3 seals. In addition, small interstitial lymphoid aggregates in the cortex and the connective tissue adjacent to larger vessels were present in 2 seals and the submucosa of the ureter in 1 seal.

DISCUSSION

Body weight and age

For the range of ages represented by these data, weight changes were accurately described by the exponential growth equation, weight = $w_o r^t$, with body weight increasing by 23% per annum until at least 9–10 y of age. However, it should be noted that this growth equation has been fitted from cross-sectional data. If growth patterns have been unchanged over the lifetime of the oldest of these animals, i.e., 10 y, then the fitted growth curve will estimate the average of the growth curves of individual animals. This assumption is known as stationarity. However, many pinniped species, including the Cape fur seal, have been subject to periodic harvest (Wickens *et al.*, 1991) and compete with a growing fishing industry (Wickens *et al.*, 1992). When the effects of anthropogenic activity on pinniped populations are taken into consideration, the above assumption must be questioned. Furthermore, our limited data ($n = 30$ seals) do not show evidence of age-dependent changes in the allometric relationship. However, we would expect to find such changes in a larger sample size, e.g., rapid growth of juveniles and reduced growth at physical maturity (Stewardson, unpubl. data).

Organ size

The size of visceral organs in relation to body weight in some pinnipedia and cetacea have been discussed (Slijper, 1958; Gihr & Pilleri, 1969; Bryden, 1971, 1972; Payne, 1979). It has been shown that variation in blubber thickness attributed to age and season can have a considerable effect on relative organ weights in male pinnipeds (Schusterman & Gentry, 1971). Such limitations should be kept in mind when interpreting the significance of relative organ weights, especially when comparing results with other data sets.

Relative organ weights in adult Cape fur seals were slightly higher than percentages of body weight previously calculated for adult Antarctic fur seals (heart 0.5%; lungs 0.9%; liver 3.4%; kidneys 0.5%; spleen 0.3%) (Payne, 1979), with some exceptions. The Cape fur seal spleen was slightly smaller, and the lungs were considerably larger.

Antarctic fur seals feed predominantly on Antarctic krill, *Euphausia superb*. These pelagic crustaceans are *c.* 5 cm in length (small body size), form great swarms at or near the water surface (concentrated food source), and move slowly in the water column (easy to catch). The krill is usually captured at night from shallow waters. In contrast, Cape fur seals pursue large, fast prey, predominantly teleost fish. Average dive depth is generally greater when compared with Antarctic fur seals (Costa, 1991). We suggest that increased lung capacity (maximum oxygen-carrying capacity) would be advantageous to Cape fur seals because of their energetically costly foraging behaviour.

The relative size of organs was similar to those of terrestrial carnivores, although the liver and kidneys were notably larger. It has been suggested that large liver size may be a response to the high metabolic demands of deep diving, possibly facilitating the metabolism of nitrogenous products, fats and carbohydrates; whereas large kidney size is possibly related to high salt intake and the need to produce great quantities of urine (Slijper, 1958; Scheffer, 1960; Evans, 1993; Bryden 1972).

Organ growth

We have estimated the coefficient in the regression of log organ weight on log body weight. It should be noted that a different relationship would be obtained which would be represented on the graphs by a slightly steeper slope, if the regression were log body weight on log organ weight. For the present application, there is an underlying functional relationship.

For the range of ages represented in this study, organ weight increased at a rate of between 25% and 33% per annum until at least 9–10 y of age, with the exception of the intestines, where exponential increase appeared to have ceased by about 7 y. The exponents b for the lungs, stomach, intestine and kidneys were not significantly different from 1, suggesting that these organs increased in proportion to the body. However, the heart, liver and spleen had exponents $b > 1$, suggesting that these organs increased at a faster rate than the body. The functional importance of the latter organs to the general physiology of the seal is therefore of great interest, and warrants further investigation. Although slight changes may occur in those organs, whose functional significance changes during postnatal life (Bryden, 1971), small sample size prevented detection of possible differences between or within growth phases.

Although detailed information on organ growth in pinnipeds is limited, differences in the relative size and relative growth of certain organs such as the spleen, liver and kidneys, have been noted between different groups of marine mammals, and between marine mammals and terrestrial mammals (Bryden, 1972). Bryden (1971) investigated organ growth in southern elephant seals, *Mirounga leonina*; however, his study was based on fat-free body weight, thus preventing direct comparison with the present data set. Payne (1979) investigated organ growth in Antarctic fur seals, but his interpretation of growth patterns did not include statistical evidence, thus his attention has not been directed at scientifically interesting features that may be independent of sampling effects.

Gross and microscopic anatomy

Heart

The anatomy and physiology of the heart in some pinnipeds have been described (Bryden & Lim, 1969; Drabek, 1975, 1977; King, 1977, 1983). Apart from its broad, flat shape and large aortic bulb, the Cape fur seal heart resembled that of terrestrial carnivores (Evans, 1993). Histologically, the heart was similar to other marine mammals and, like that of other pinnipeds, differed from those of cetacea in not having unusually thick endocardium and prominent Purkinje cells (Simpson & Gardner, 1972; Haldiman & Tarpley, 1993).

Lung

The multilobed lung was similar to other terrestrial carnivores (Evans, 1993), although slightly larger. The division of the lung into 4 right lobes and 2 left lobes was typical of other terrestrial carnivores, yet differed from some pinniped species. For example, the ribbon seal, *Phoca fasciata*, harp seal, *Phoca groenlandica*, and the Largha seal, *Phoca largha*, have little or no lobation (Sokolov *et al.*,, 1968; Tarasoff & Kooyman, 1973; King, 1983). General features were otherwise typical of other pinnipeds (Harrison & Kooyman, 1968; Denison & Kooyman, 1973; Boshier & Hill, 1974; King, 1983).

Histological features of the lungs were typical of otariid seals (Simpson & Gardner, 1972; Denison & Kooyman, 1973), with notable features being prominent fibrous septa, prominent smooth muscle bundles and ample lymphoid tissue. Cartilaginous support extended to the level of the alveolar sacs, presumably preventing the passive collapse of airways when diving and facilitating the quick exchange of air (Kooyman & Andersen, 1969; King, 1983).

Liver

The liver was large, multilobed and had deep natural fissures. The extent of lobation appears to vary among pinniped species, with 5–8 lobes recorded within the Otariidae (Owen, 1830–31; Murie, 1874; present study). Apart from its relatively large size, and the arrangement of the caudate lobe, the liver was typical of terrestrial carnivores (Brody, 1945; King, 1983; Evans, 1993). Unlike cetaceans, a gall bladder was present in Cape fur seals.

Earlier studies examining the histological structure of the otariid liver record few special features apart from the common presence of iron pigments in hepatocytes and the presence of tall columnar, mucus secreting, bile duct epithelial cells (Simpson & Gardner, 1972; Eastman & Coalson, 1974; Britt & Howard, 1983; Lowenstine & Osborn, 1990). The presence of iron was not determined in the present study but the presence of tall columnar epithelial cells, apparently containing mucus, were present in large bile ducts.

Spleen

A typical mammalian spleen was present (Evans, 1993). Although the pinniped spleen is said to be moderately large (Slijper, 1958, 1962), percentages calculated for the adult Cape fur seal at 0.2–0.4% (present study), did not differ greatly from terrestrial mammals, at around 0.3% (Bryden, 1971). Large spleen size reported in other species of pinnipeds, such as the southern elephant seal may be a response to the high metabolic demands of deep diving, assisting in the regulation of blood pressure and respiration (Andersen, 1966; Bryden & Lim, 1969; Gihr & Pilleri, 1969).

The histological features of the Cape fur seal spleen were similar to those previously reported in other pinnipeds (Simpson & Gardner, 1972; Schumacher & Welsch, 1987; Lowenstine & Osborn, 1990). The thick capsule, well developed trabeculae, arrangement of the red and white pulp and plentiful plasma cells found in the present study were in keeping with findings of the detailed report of Schumacher and Welsch (1987). However, eosinophils and plentiful macrophages in the marginal zone of follicles were not detected in the present study. These differences may indicate differing levels of immune stimulation, disease or parasitism; or may represent species differences. Similarly, the earlier study found evidence of erythropoiesis and thrombopoiesis in the red pulp, neither of which was conspicuous in the current study. This may be due to differences in age, as haematopoiesis has been reported elsewhere to be common in young seals (Lowenstine & Osborn, 1990); disease status or species.

Stomach

The stomach was a single chamber, with an indistinct cardia and fundus. As with other pinnipeds, digestion and absorption is a rapid process, occurring within 24–48 h (D. Miller, pers. comm.; Murie & Lavigne, 1985, 1986; Olsen *et al.*,, 1996). Considering that the Cape fur seal feeds predominantly on soft food items (teleost fish and squid) which are swallowed whole, in chunks or in strips (Stewardson unpubl. data), abundant gastric glands, a small pyloric ostium and a well developed pyloric sphincter would ensure that food items are well triturated before entering the intestine (Eastman & Coalson, 1974).

General histological features of the stomach were in keeping with those previously reported for the Weddell seal (Eastman & Coalson, 1974). Abundant parietal cells have been found previously to be predominant in porpoises and sea lions (Simpson & Gardner, 1972), as they were in Cape fur seals.

Small and large intestine

The small intestine of pinnipeds is remarkably long (King, 1983). In most terrestrial carnivores the length of the small intestine to length of body is only 5–6 : 1 (King, 1983), yet in the adult Cape fur seal the ratio is 15 : 1 (present study). It has been suggested that the great length of the pinniped intestine is a response to large body size and high metabolic demands as the longer the gut, the greater is the surface area for food absorption (Bryden, 1972; Eastman & Coalson, 1974). The long guts in pinnipeds is also believed to increase the time available for enzymatic breakdown (Olsen *et al.*, 1996).

The histological organisation of the small and large intestine was typical of pinnipeds but the length of the small intestinal villi appeared excessive. Unusually long villi were not reported in previous descriptions of the gastrointestinal tract of the Weddell seal, *Leptonychotes weddellii*, crabeater seal, *Lobodon carcinophagus*, and California sea lion (Simpson & Gardner, 1972; Eastman & Coalson, 1974; Schumacher & Welsch, 1995). As the results of the present study are based on examination of a single animal which had evidence of underlying gastrointestinal inflammation it cannot be assumed that these findings are characteristic of the species. Villous hypertrophy, distortion and fusion are lesions sometimes seen with chronic mucosal inflammation, and it cannot be ruled out that the villi of the seal in the present study were abnormal (Lee & Toner, 1980).

Kidneys

The anatomy and physiology of the kidney in some species of pinnipeds have been described (Anthony & Liouville, 1920; Depocas *et al.*, 1969; Arvy & Hidden, 1973; Bester, 1975; Vardy & Bryden, 1981; King, 1983). In the Cape fur seal, the kidney is made up of a large number of reniculi, with each unit containing a complete cortex, medulla and calyx (Bester, 1975; present study). Only pinnipeds and cetaceans have truly reniculate kidneys, presumably a response to large body size and the ability to concentrate urine (Vardy & Bryden, 1981).

The histological features of the kidney of the Cape fur seal were similar to those recorded previously (Bester, 1975). A sporta perimedullaris musculosa was not identified in the present study, nor in the study of Bester (1975); however, it is possible that collagenous and muscular tissue present at the corticomedullary junction was not identified in this study due to the sole reliance on H & E stained sections. The presence of lymphoid cells in the majority of seal kidneys examined probably indicates low grade nephritis as the presence of lymphoid cells has not been reported in previous studies of pinniped kidneys, including those of the Cape fur seal.

CONCLUSIONS

Information presented in this study contributes to earlier descriptions of the pinniped viscera, and provides new data of potential benefit to veterinary practitioners and students of mammalian physiology. The basic features of the viscera were similar to those of other otariids (Murie, 1874; Green, 1972; Odell, 1981; Vaz-Ferreira, 1981) and phocids (Owen, 1830–1831; Hepburn, 1912; St-Pierre, 1974). Apart from the liver and kidneys, relative organ size was similar to those of terrestrial carnivores, and most organs increased in proportion to body weight. Notwithstanding post mortem autolysis of some tissues and sole reliance on H & E stained sections, examination of the salient histological features of the tissues was possible. The histological organisation of the viscera was generally consistent with that previously described for this species (Denison & Kooyman, 1973; Bester, 1975; Schumacher & Welsch, 1987) and other pinnipeds (Simpson & Gardner, 1972; Lowenstine & Osborn, 1990).

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PART 2

GENERAL BIOLOGY

AGE AND GROWTH

CHAPTER 3

Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part one, external body

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ABSTRACT

Morphology, relative size and growth of the Cape fur seal, *Arctocephalus pusillus pusillus*, from the coast of southern Africa are described. External body measurements (n = 12 linear variables) were examined in relation to standard body length (SBL) and chronological age (y) using linear regression. Animals ranged from < 1 mo to ≥ 13 y. Of the 149 animals in the study 39 were animals of known-age; 34 were aged from counts of incremental lines observed in the dentine of upper canines (i.e., range 1–10 y); 10 were identified as adults > 12 y (i.e., pulp cavity of the upper canine closed); and 66 were not aged. Counts of growth layer groups in the dentine of upper canines were found to be highly reproducible. At birth, male Cape fur seals are 35% (*c.* 69 cm) of their mean adult size. At puberty, they are 57% (*c.* 113 cm). The foreflippers are relatively long measuring 25–26% (*c.* 18 cm) of standard body length (SBL) in pups, and 24% (*c.* 48 cm) of SBL in adults. The hind flippers are considerably shorter measuring 19% (*c.* 13 cm) in pups, and 14.5% (*c.* 29 cm) in adults. Axillary girth is usually about 57–67% of SBL. For the range of ages represented in this study, growth of SBL was rapid during the early postnatal period with a significant growth spurt occuring at the onset of puberty (2–3 y). The rate of growth slowed significantly between 6 and 7 y. A weak growth spurt was observed at 9 and 10 y (social maturity) but could not be examined statistically. Growth slowed thereafter, i.e., the mean for males > 10 y (including unaged animals > 200 m) was 199 cm. Relative to SBL, facial variables and the fore/hind limbs scaled with negative slope relative to SBL or were negatively allometric; tip of snout to genital opening scaled with positive slope; and tip of snout to anterior insertion of the foreflipper was positively allometric. Relative to age, body variables scaled with negative slope or were negatively allometric. In animals 1–10 y, SBL was found to be a very ‘rough indicator’ of age and age group.

Key words: Pinnipeds; body; growth; allometry

INTRODUCTION

Knowledge of the physical growth of pinnipeds is fundamental to understanding biological, evolutionary and functional links within and between populations.

Within the Otariidae (fur seals and sea lions) quantitative descriptions of growth in body length based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), are available for several species including *Eumetopias jubatus*, northern (Steller) sea lion (Fiscus, 1961; Thorsteinson & Lensink, 1962; Calkins & Pitcher, 1983; Loughlin & Nelson, 1986; McLaren, 1993), *Arctocephalus gazella*, Antarctic fur seal (Payne 1979; Krylov & Popov, 1980; McLaren, 1993); *Callorhinus ursinus*, northern fur seal (Scheffer & Wilke, 1953; Bychkov, 1971; Bigg, 1979; Lander, 1979; McLaren, 1993; Trites & Bigg, 1996); and *Otaria byronia*, South American sea lion (Rosas, Haimovici & Pinedo, 1993). Apart from studies by Scheffer & Wilke (1953) and Payne (1997), information on growth of other external body measurements is scant, e.g., axillary girth; length of limbs.

Physical growth in the northern fur seal has been studied in most detail. The general growth curve for this species is presumably representative of all highly polygynous male otariids. Male pups measure *c.* 66 cm at birth and grow at a steady rate (Scheffer & Wilke, 1953). Growth increases suddenly at 3–4 y (puberty) and slows soon after attainment of social maturity (McLaren, 1993). Estimated asymptotic length is *c.* 189 cm for males > 4 y, and is reached by *c.* 12 y in most animals (McLaren, 1993).

Here we examine the body measurements of 149 male Cape fur seals, *Arctocephalus pusillus pusillus*, from Southern Africa. Specific objectives were to: (i) describe the general morphology of the animal; (ii) quantify growth of body measurements (n = 12 variables) relative to standard body length (n = 134 animals) and chronological age (n = 83 animals); and (iii) determine if standard body length is a useful indicator of age. This study is the first in a series of papers initiated to develop baseline descriptions of Cape fur seal morphology and to examine growth patterns.

Information on growth in body size is available for Cape fur seals (Rand, 1956); however, this information is based on measurements that were aged physiologically (cranial suture age) rather than chronologically (y).

MATERIALS AND METHODS

Collection of specimens

Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). From this collection, 110 males were selected for examination (Appendix 3.1). Apart from specimens collected before May 1992 (n = 38), all specimens were collected by the first author. One animal (PEM2238) was collected NE of the study area, at Durban.

The sample was supplemented with measurements from 39 males from Marine and Coastal Management (MCM), Cape Town. These measurements were from animals that had been tagged as pups, and were therefore of known-age (1–13 y). MCM seal specimens are accessioned as AP followed by a number.

Body measurements

Standard necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). Upper canines were collected for age determination.

Measurements (12 variables) were taken to the nearest 5 mm using a flexible tape measure or vernier callipers as appropriate (Fig. 3.1). Although body weight and blubber thickness were recorded, these measurements were not included in the analysis because they can vary according to physiological condition, e.g., body condition is influenced by seasonal fluctuations in food supply, illness or injury, and breeding condition. Apart from specimens collected before May 1992, all PEM measurements were recorded by the first author. The majority of MCM measurements were recorded by the third author.

Age determination

The age of animals was estimated from counts of growth layer groups (GLGs) observed in the dentine of thin tooth sections (Fig. 3.2). Upper canines were sectioned longitudinally using a circular diamond saw. Sections were ground down to 280–320 µm, dehydrated, embedded in resin and viewed under a stereomicroscope in polarised light (Oosthuizen, 1997). Each section was read by one individual five times, without knowledge of which animal was being examined (repeated blind counts). Ages were rounded off to the nearest birth date. The median date of birth was assumed to be 1 December (Shaughnessy & Best, unpubl. report). The median of the five readings was used as an estimate of age. Outliers were discarded as reading errors.

Currently, examination of tooth structure is the most precise method of age determination in pinnipeds (McCann, 1993), including Cape fur seals Oosthuizen (1997). However, this method can only be used in animals ≤ 13 y. At about 13 y of age, closure of the pulp cavity terminates tooth growth.

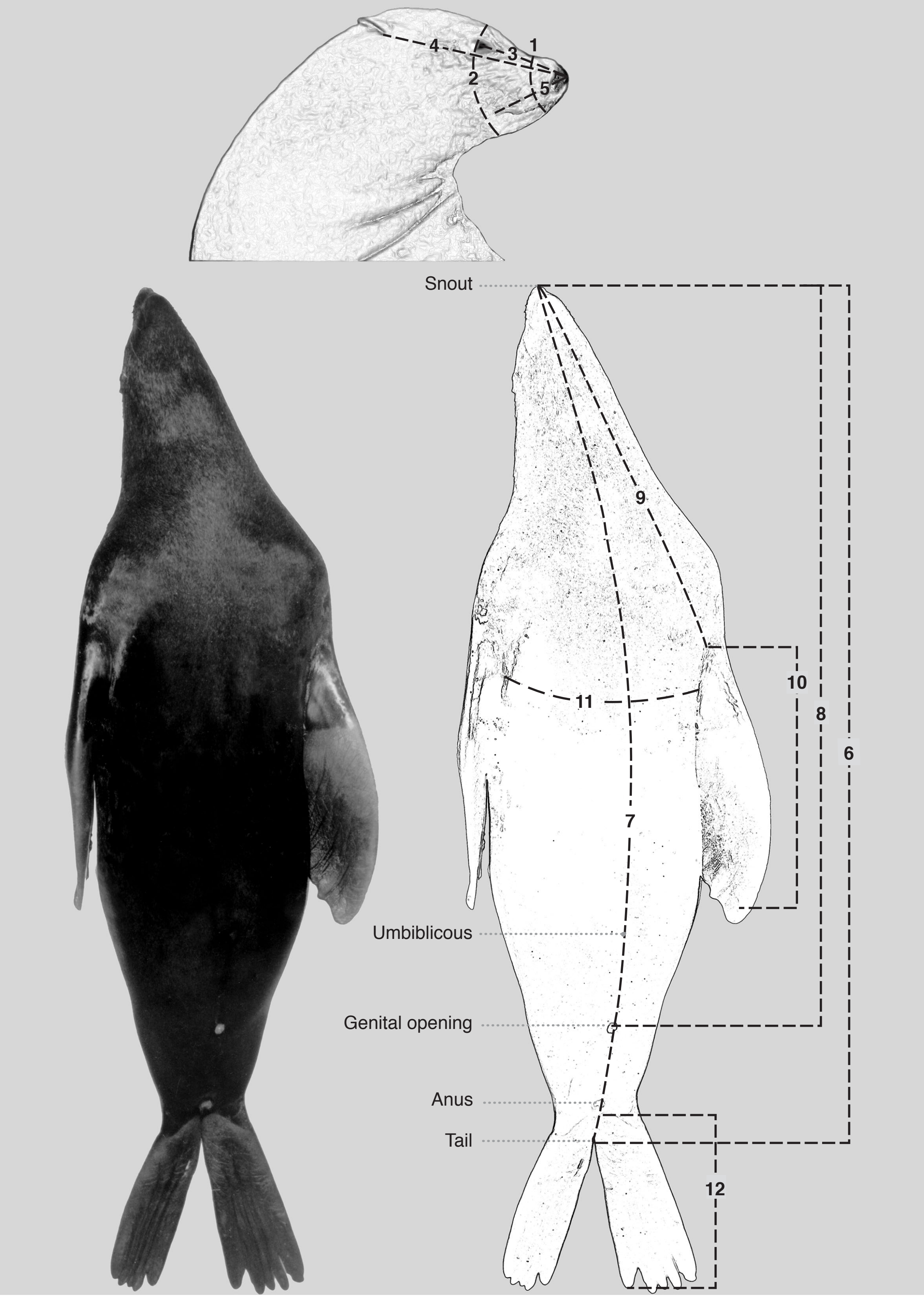

Fig. 3.1 Diagram of a male Cape fur seal showing how individual body measurements were taken. All measurements were taken with the animal lying on its back.
1. Circumference of head at canine; 2. circumference of head at eye; 3. tip of snout to centre of eye; 4. tip of snout to centre of ear; 5. tip of snout to angle of gape; 6. standard body length (straight line from tip of snout to tip of tail with animal lying on its back); 7. ventral curvilinear length (tip of snout to tip of tail over body curve); 8. tip of snout to genital opening; 9. tip of snout to anterior insertion of the foreflipper; 10. length of foreflipper (anterior insertion to tip of first claw); 11. axillary girth; and 12. length of hind flipper (anterior insertion to tip of first claw).

Of the 149 animals in the study: (i) 39 were known-age MCM animals; (ii) 34 were aged from counts of incremental lines observed in the dentine of upper canines, i.e., range 1–10 y; (iii) 10 were identified as adults > 12 y (i.e., pulp cavity of the upper canine closed); and (iv) 66 were not aged.

For this study, the following age groups were used: pup (< 1 mo to 6 mo); yearling (7 mo to 1 y 6 mo); subadult (1 y 7 mo to 7 y 6 mo); and adult (≥ 7 y 7 mo) (Table 3.1). Very old animals of known-age were not available for examination (estimated longevity is *c.* 20 y).

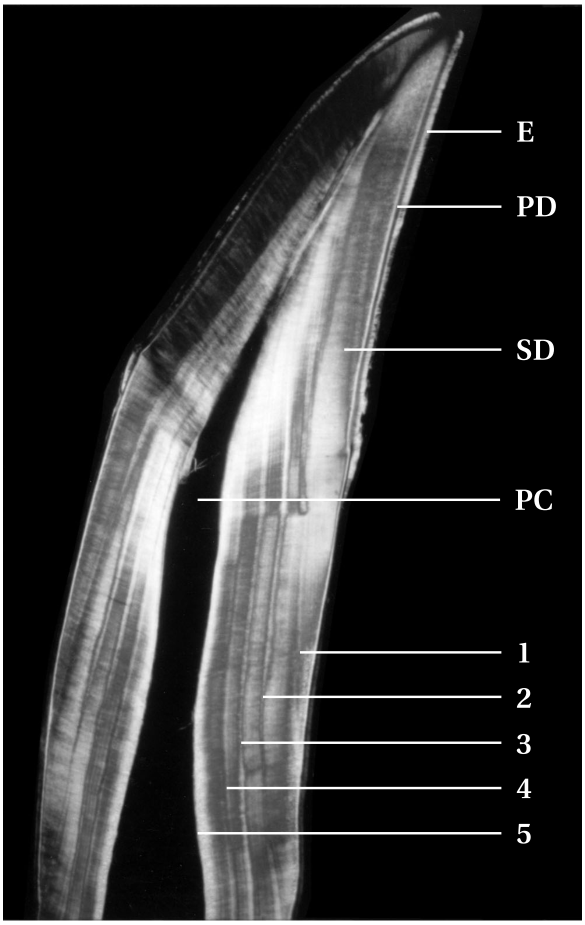

Fig. 3.2 Longitudinal section of a upper canine from a Cape fur seal, showing 5 growth layer groups (GLGs).
E, enamel; PD, primary/pre-natal dentine; SD, secondary dentine; PC, pulp cavity; 1–5, successive growth layer groups (GLGs) in the secondary dentine.

Statistical analysis

Body variable expressed in relation to standard body length

Growth in body measurement, relative to standard body length (SBL), was calculated as follows, using paired samples only:

body measurement (mm)/SBL (mm) × 100%

As the approximate variance of the ratio estimate is difficult to calculate, percentages must be interpreted with caution, i.e., both y and x vary from sample to sample (Cochran, 1977, p. 153).

Body length as an indicator of age

The degree of linear relationship between log body measurement, log SBL and age (y) was calculated using the Spearman rank-order correlation coefficient. Linear discriminant function analysis was used to predict the likelihood that an individual seal will belong to a particular age group using one independent variable, body length. Here we use the Mahalanobis squared distance of observation x to the mean of group i:

$$D_i^2(x) = -2\left[\bar{x}_i^T S^{-1} x - \tfrac{1}{2}\bar{x}_i^T S^{-1} \bar{x}_i\right] + x^T S^{-1} x$$

where S is the pooled covariance matrix. An observed value x is classified into the age group (pup, yearling, subadult, adult) which gives the smallest calculated Mahalanobis squared distance. This is equivalent to the term in square brackets being maximised for group membership (Anderson, 1984).

Bivariate allometric regression

The relationship between value of body measurement and: (i) SBL and (ii) age (y), was investigated using the logarithmic (base e) transformation of the allometric equation, $y = ax^b$, which may equivalently be written as $\log y = \log a + b \log x$. 'Robust' regression (Huber M-Regression) was used to fit straight lines to the transformed data. The degree of linear relationship between the transformed variables was calculated using the Spearman rank-order correlation coefficient, r (Gibbons & Chakraborti, 1992). It is important to note that the regression equations relating to overall growth do not consider variations in body condition that are known to occur in this species (e.g., Rand, 1956).

Statistical tests of hypotheses about model parameters are only valid if the model assumptions hold (i.e., errors are independently and identically Normally distributed with zero mean and variance σ^2) (Weisberg, 1985, p. 24, 156). The standard approach is to first examine the residules versus fitted plot. If this is a random scatter about zero, then the Normality assumption can be assessed. In the present study, the following tests for Normality were used: (i) Anderson-Darling, (ii) Ryan-Joiner and (iii) Kolmogorov-Smirnov.

The appropriate test statistic was calculated as follows:

$$T = \frac{\hat{\beta} - 1}{S.E.(\hat{\beta})}$$

where T has a student t distribution with $d.f. = n–2$.

The following hypotheses were tested:

$H_0 : \hat{\beta} = 1$ (isometric) versus $H_1 : \hat{\beta} \neq 1$ (either positively or negatively allometric); $H_1 : \hat{\beta} > 1$ (positively allometric); $H_1 : \hat{\beta} < 1$ (negatively allometric).

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23); Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997), and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

Terminology

Puberty is when reproduction first becomes possible (production of sperm in quantity), and social maturity is the age when the animal reaches full reproductive capacity (physically able to establish and maintain a harem).

RESULTS

Age determination (intra-observer variability)

Counts of GLGs were found to be highly reproducible. Of the 34 PEM animals for which GLGs were counted, 14 (41%) had all five readings equal; 16 (47%) had one reading out of 5 different from the mode; and 4 (12%) had 2 readings out of 5 different from the mode (Table 3.2).

Table 3.1 *The age distribution of Cape fur seals*

Age group	Age[a] (y)	Frequency	Percentage
Pup[b]	0	3	3.6
Yearling	1	8	9.6
Subadult	2	5	6.0
	3	5	6.0
	4	9	10.8
	5	5	6.0
	6	10	12.1
	7	11	13.3
Adult	8	6	7.2
	9	5	6.0
	10	4	4.8
	13	2	2.4
	> 12	10	12.1
Total		**83**	**100**

[a] **Animals** 1–10 y: 37 MCM animals were of known-age; 34 PEM animals were aged from counts of incremental lines observed in the dentine of upper canines.
Animals > 12 y: 2 MCM animals were 13 y; 10 PEM males were > 12 y, i.e., the pulp cavity of the upper canine was closed.
[b] < one month of age.

Age determination (variability between known-age and canine aged animals)

Standard body length was selected to investigate whether MCM (animals of known-age) and PEM (canine aged animals) animals were similar with respect to age. When comparing the (robust) regression line for MCM SBL on age with PEM SBL on age, partial t-tests indicate that age is important (t = 7.07, p = 0.000), even after adjusting for group and age-group interaction; but they provide little information on group (t = -0.82, p = 0.42) and age-group interaction (t = 0.87, p = 0.58), hence one straight line can be fitted to the data. These statistical conclusions were verified by examining graphical displays of fitted values and residuals. Thus PEM and MCM animals were not significantly different with respect to age.

This conclusion is supported by the sequential F test, provided the sequence of terms added sequentially (first to last) was: (i) none (i.e., fitting a line parallel to the x axis); (ii) age (F = 817.69, p = 0.000) (one straight line); (iii) museum (ie., MCM and PEM) (F = 0.0659, p = 0.7984) (two parallel lines); (iv) age × museum (F = 0.1883, p = 0.6661) (two lines not necessarily parallel).

Table 3.2 *Intra-observer variability (number of tooth readings different from the mode)*

Range	0	1	2	Total
0	14 (100%)	0	0	14 (100%)
1	0	14 (82%)	3 (18%)	17 (100%)
2	0	1 (50%)	1 (50%)	2 (100%)
3	0	1 (100%)	0	1 (100%)
Total	**14 (41%)**	**16 (47%)**	**4 (12%)**	**34 (100%)**

Age was taken as the mode of the 5 readings for each animal. For our data, the mode and median were concurrent.

Bivariate allometric regression

Regression statistics for body measurements on SBL and age (1–10 y) are given in Appendix 3.3 and 3.4. Overall, correlation coefficients were moderately to strongly positive, i.e., most points on the scatter plot approximated a straight line with positive slope, $r \geq 0.70$. Exceptions included tip of snout to centre of eye (V3) with age and SBL (r = -0.008 and 0.15 respectively); tip of snout to angle of gape (V5) with age (r = 0.56); circumference of head at canine (V1) with age (r = 0.59).

Although correlation coefficients indicate that linearity was reasonably well approximated for most variables by log-log transformations, a linear relationship did not necessarily best describe the relationship.

Growth of body variables

Most variables were significantly positively correlated with each other, $r \geq 0.68$ (Appendix 3.2). Exceptions were: (i) tip of snout to centre of eye (V3) with all variables; (ii) circumference of head at eye (V2) with tip of snout to angle of gape (V5) ($r = 0.61$); and (iii) circumference of head at canine (V1) with tip of snout to angle of gape (V5) ($r = 0.63$).

Circumference of head at canine (V1)

Growth of circumference of head at canine (V1) was variable relative to age, $r = 0.59$ (Appendix 3.4). Overall growth expressed negative allometry relative to SBL and age (Appendix 3.3, 3.4), increasing by 57% at 10 y relative to pups (RTP) (Table 3.3). Growth increment decreased with increasing SBL until about 7 y (*c.* 15% of SBL) (Table 3.4).

Mean SBL of males > 10 y (including unaged animals > 200 cm) was 31.8 ± 1.2 cm ($n = 5$). Maximum recorded value was 35.0 cm (animal AP3017, SBL 209 cm, 12 y 11 mo).

Circumference of head at eye (V2)

Growth of circumference of head at eye (V2) was rapid during the early postnatal period and continued to increase until at least 13 y. Overall growth expressed negative allometry relative to SBL and scaled with negative slope relative to age ($b = 0.12$) (Fig. 3.3a; Appendix 3.3), increasing by 65% at 10 y (RTP) (Table 3.4). Growth increment decreased with increasing SBL until about 7 y (*c.* 22% of SBL) (Table 3.3).

Mean SBL of males > 10 y (including unaged animals > 200 cm) was 45.8 ± 1.8 cm ($n = 6$). Maximum recorded value was 53.0 cm (animal PEM676, SBL 197 cm).

Tip of snout to centre of eye (V3)

Growth of tip of snout to centre of eye (V3) was highly variable relative to age, $r = -0.008$, and SBL, $r = 0.15$ (Appendix 3.3 and 3.4). Growth increment decreased with increasing SBL until about 9 y (*c.* 5% of SBL) (Table 3.3).

Mean SBL of males > 10 y (including unaged animals > 200 cm) was 10.4 ± 0.6 cm ($n = 10$). Maximum recorded value was 14.4 cm (animal PEM2194, SBL 194 cm).

Tip of snout to centre of ear (V4)

Growth of tip of snout to centre of ear (V4) was rapid during the early postnatal period and continued to increase until at least 13 y (Table 3.3 and 3.4). Overall growth expressed negative allometry relative to SBL and scaled with negative slope relative to age ($b = 0.04$) (Fig. 3.3b; Appendix 3.3), increasing by 70% at 10 y RTP (Table 3.4). Growth increment decreased with increasing SBL until about 7 y (*c.* 12% of SBL) (Table 3.3).

Mean SBL of males > 10 y (including unaged animals > 200 cm) was 22.7 ± 0.8 cm ($n = 7$). Maximum recorded value was 25.2 cm (animal AP3125, SBL 204 cm, 13 y).

Tip of snout to angle of gape (V5)

Growth of tip of snout to angle of gape (V5) was variable relative to age, $r = 0.56$ (Appendix 3.4). Overall growth scaled with negative slope relative to SBL ($b = 0.64$) and expressed negative allometry relative to age (Appendix 3.4), increasing by 55% at 10 y RTP (Table 3.4). Growth increment decreased with increasing SBL until about 7 y (*c.* 6% of SBL) (Table 3.3).

Mean SBL of males > 10 y (including unaged animals > 200 cm) was 13.2 ± 0.7 cm ($n = 7$). Maximum recorded value was 15.0 cm (animal PEM676, SBL 197 cm).

Standard body length (V6)

Growth of SBL (V6) was rapid during the early postnatal period with a significant growth spurt between 2 and 3 y (two sample t test[1]: p-value = 0.008; df = 5).

The rate of growth slowed significantly between 6 and 7 y (two sample t test[1]: p-value = 0.011; df = 9). A weak growth spurt was observed at 9 and 10 y but could not be examined statistically, i.e., this secondary growth spurt may be attributed to sampling error. Growth increased by 164% at 10 y RTP (Table 3.4).

Considering that the 13 y old males measured 206.5 ± 2.5 cm ($n = 2$), and mean SBL of males > 10 y (including unaged animals > 200 cm) was 199.4 ± 3.6 cm ($n = 17$), growth appears to slow after attainment of social maturity (Table 3.3).

Tip of snout to genital opening (V8)

Growth of tip of snout to genital opening (V8) was rapid during the early postnatal period and continued to increase until at least 13 y (Table 3.3 and 3.4). Growth increased by 186% at 10 y RTP (Table 3.4). In subadults and adults, mean value remained at about 86% of SBL (Table 3.3). Overall growth scaled with weak positive slope relative to SBL ($b = 1.04$) and negative slope relative to age ($b = 0.02$).

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[1] The two sample t test assumed unequal variances.

Table 3.3 *Summary statistics for body variables (1–12), according to age (y) and age group.* **Data presented as mean body measurement in cm ± S.E., followed by coefficient of variation in round brackets, and body variable expressed as a percentage of SBL. Maximum value of each variable (males of unknown-age) is also presented.**

Age group	Age (y)	n[a]	Var 1	Var 2	Var 3[c]	Var 4	Var 5	Var 6	Var 7[d]	Var 8	Var 9	Var 10	Var 11[e]	Var 12
Pup	< 1	3	16.9 ± 1.1 (11.3) 24.4%	24.1 ± 1.4 (10.3) 34.7%	9.1 ± 0.9 (16.4) 13.1%	11.8 ± 0.1 (2.1) 17.0%	7.1 ± 0.7 (16.5) 10.3%	69.3 ± 2.8 (7.1) –	70.9 ± 3.6 (8.7) –	55.6 ± 1.7 (5.3) 80.2%	31.7 ± 0.9 (4.8) 45.7%	17.6 ± 1.6 (16.2) 25.4%	39.6 ± 3.5 (15.5) 57.1%	13.3 ± 0.7 (9.4) 19.2%
Yearling	1	8	19.6 ± 0.9 (12.5) 21.6%	27.9 ± 1.4 [7] (13.2) 30.9%	8.3 ± 0.6 [7] (18.2) 9.0%	13.7 ± 0.4 (7.6) 15.1%	7.7 ± 0.3 (12.3) 8.4%	90.8 ± 2.4 (7.4) –	95.3 ± 3.9 [3] (7.1) –	75.9 ± 2.2 (8.1) 83.7%	41.1 ± 1.7 (11.6) 45.3%	22.4 ± 1.2 (15.0) 24.7%	53.1 ± 4.6 (24.4) 58.5%	15.1 ± 0.4 (8.0) 16.6%
Subadult	2	5	21.1 ± 1.1 (12.1) 22.5%	30.8 ± 1.6 (11.7) 32.8%	10.2 ± 1.3 [4] (25.5) 10.8%	14.9 ± 0.5 (7.7) 15.9%	7.8 ± 0.4 (11.4) 8.3%	93.8 ± 1.9 (4.5) –	– [0]	79.6 ± 2.4 (6.8) 84.9%	37.7 ± 0.8 (4.6) 40.2%	23.5 ± 0.4 (4.3) 25.1%	58.2 ± 3.1 (11.8) 62.0%	16.0 ± 0.6 (8.3) 17.0%
	3	5	22.2 ± 0.5 (4.8) 19.7%	32.2 ± 0.8 (5.3) 28.5%	10.7 ± 1.2 [4] (23.2) 9.6%	17.1 ± 0.4 (5.8) 15.2%	8.6 ± 0.6 (14.3) 7.6%	112.8 ± 4.0 (8.0) –	– [0]	98.1 ± 2.1 (4.9) 87.0%	48.9 ± 2.1 (9.5) 43.3%	27.4 ± 1.4 (11.2) 24.3%	73.9 ± 2.0 (6.2) 65.5%	18.1 ± 0.8 (9.3) 16.0%
	4	9	24.1 ± 0.6 (7.6) 19.6%	34.3 ± 0.5 (4.8) 27.7%	9.1 ± 0.5 (17.7) 7.6%	18.3 ± 0.5 (7.9) 14.8%	9.9 ± 0.3 (7.8) 7.9%	124.3 ± 5.0 [8] (11.4) –	– [0]	107.2 ± 3.6 [8] (9.5) 86.2%	52.5 ± 1.7 (9.8) 42.6%	30.1 ± 1.1 (11.0) 24.5%	80.2 ± 2.3 (8.5) 64.7%	18.6 ± 0.5 (8.8) 15.2%
	5	5	24.0 ± 0.4 [4] (3.4) 17.9%	34.8 ± 1.4 [4] (7.9) 26.8%	9.9 ± 0.7 (15.4) 6.6%	18.8 ± 0.9 (11.3) 13.4%	8.6 ± 0.7 [3] (14.7) 6.8%	136.5 ± 2.5 [2] (2.6) –	149.7 ± 2.7 [3] (3.2) –	124.5 ± 4.8 (8.7) 84.4%	62.7 ± 4.2 (14.9) 40.5%	35.7 ± 1.4 (9.0) 23.9%	85.8 ± 0.8 [2] (1.2) 62.8%	21.7 ± 1.3 [3] (10.1) 15.0%
	6	10	24.9 ± 0.6 (7.8) 17.0%	37.1 ± 0.8 (7.0) 25.3%	10.4 ± 0.5 [8] (14.6) 7.2%	19.3 ± 0.5 (8.2) 13.0%	10.2 ± 0.3 [9] (7.6) 7.0%	145.8 ± 1.4 [9] (2.8) –	155.3 ± 5.2 [3] (5.8) –	126.7 ± 1.7 (4.2) 87.2%	65.5 ± 3.4 (16.3) 43.6%	33.6 ± 0.9 [9] (7.7) 23.0%	91.4 ± 2.1 [9] (6.8) 62.7%	21.2 ± 0.4 [9] (5.9) 14.5%
	7	11	23.7 ± 0.8 [10] (10.6) 15.1%	34.7 ± 0.8 [10] (7.2) 22.3%	9.0 ± 0.6 [7] (18.6) 6.2%	18.2 ± 0.4 (7.7) 11.5%	9.3 ± 0.5 (16.7) 6.3%	157.5 ± 3.4 [8] (6.2) –	158.5 ± 4.3 [5] (6.0) –	132.5 ± 2.5 (6.3) 84.9%	71.8 ± 2.1 (9.6) 45.8%	34.7 ± 1.1 (10.1) 22.4%	100.2 ± 3.1 [7] (8.3) 64.4%	23.6 ± 0.7 [10] (9.1) 15.2%
	2–7	**45**	**23.6 ± 0.3 [43]** **(9.5) 17.9%**	**34.5 ± 0.5 [43]** **(8.9) 26.2%**	**9.8 ± 0.3 [37]** **(18.5) 7.7%**	**18.0 ± 0.3** **(10.5) 13.6%**	**9.3 ± 0.2 [42]** **(14.1) 7.2%**	**131.7 ± 3.8 [37]** **(17.5) –**	**155.2 ± 2.6 [11]** **(5.5) –**	**115.7 ± 2.9 [44]** **(16.5) 86.0%**	**59.2 ± 2.0** **(22.2) 43.4%**	**31.6 ± 0.7 [44]** **(15.3) 23.6%**	**83.2 ± 2.4 [37]** **(17.5) 63.8%**	**20.2 ± 0.5 [41]** **(15.0) 15.3%**
Adult	8	6	24.2 ± 1.0 [5] (9.6) 14.8%	38.6 ± 1.8 [5] (10.5) 21.4%	8.8 ± 0.6 (16.2) 5.7%	18.9 ± 0.7 (9.2) 11.7%	9.9 ± 0.8 [5] (19.0) 6.8%	161.0 ± 3.5 [3] (3.8) –	166.0 ± 2.1 [5] (2.8) –	136.6 ± 3.1 (5.5) 85.8%	76.6 ± 2.2 (7.1) 50.1%	35.2 ± 1.6 (11.5) 21.3%	90.6 ± 4.6 [2] (7.2) 57.5%	26.0 ± 1.0 (9.7) 15.8%
	9	5	26.0 ± 0.5 [4] (4.2) 15.2%	37.4 ± 1.0 (5.8) 21.6%	8.1 ± 0.7 [4] (18.1) 4.6%	20.5 ± 0.8 (9.1) 12.0%	10.7 ± 0.4 (8.8) 6.4%	170.8 ± 2.3 [4] (2.7) –	185.8 ± 3.4 [4] (3.7) –	152.6 ± 2.6 (3.8) 89.6%	83.8 ± 5.8 (15.6) 48.4%	40.6 ± 0.9 (5.0) 24.1%	114.5 ± 2.9 [4] (5.1) 67.0%	28.2 ± 1.3 (10.1) 16.5%
	10	4	26.6 ± 1.1 [3] (7.4) 14.7%	39.7 ± 1.8 [3] (7.7) 21.9%	9.5 ± 1.1 [3] (20.7) 5.2%	20.0 ± 0.2 (1.9) 10.9%	11.1 ± 0.4 (6.7) 6.0%	182.9 ± 6.0 (6.6) –	203.7 ± 4.9 [3] (4.2) –	159.3 ± 5.4 (6.8) 87.1%	87.8 ± 8.5 (19.5) 48.1%	40.3 ± 2.1 [3] (10.2) 22.0%	111.9 ± 6.9 (12.2) 61.2%	27.1 ± 1.6 (11.7) 14.8%
	13	2	31.5 ± 3.5 (15.7) 15.3%	44.5 ± 5.5 (17.5) 21.5%	11.1 ± 0.9 (11.5) 5.3%	24.6 ± 0.6 (3.4) 11.9%	13.5 ± 0.5 (5.2) 6.5%	206.5 ± 2.5 (1.7) –	– [0]	178.5 ± 3.5 (2.8) 86.4%	91.5 ± 3.5 (5.4) 44.3%	48.4 ± 3.6 (10.5) 23.4%	– [0]	27.7 ± 1.5 (7.7) 13.4%
	8–13	**17**	**26.3 ± 0.9 [14]** **(12.2) 15.0%**	**39.2 ± 1.1 [15]** **(10.5) 21.6%**	**9.1 ± 0.4 [15]** **(18.4) 5.2%**	**20.3 ± 0.5** **(11.0) 11.6%**	**10.9 ± 0.4 [16]** **(14.7) 6.4%**	**177.7 ± 4.7 [13]** **(9.4) –**	**182.0 ± 4.9 [12]** **(9.2) –**	**151.6 ± 3.8** **(10.2) 87.4%**	**83.1 ± 2.9** **(14.1) 47.9%**	**39.5 ± 1.3 [16]** **(13.5) 22.7%**	**108.7 ± 4.1 [10]** **(12.0) 62.8%**	**27.1 ± 0.46** **(9.8) 15.3%**
Total		**73**	**68**	**68**	**62**	**73**	**69**	**61**	**29**	**72**	**73**	**72**	**58**	**69**
Mean for males > 200 cm[b] [max. value in brackets]			31.3 ± 2.0 [35.0] *n* = 3	44.3 ± 3.2 [50.0] *n* = 3	11.8 ± 0.6 [13.0] *n* = 4	24.4 ± 0.4 [25.2] *n* = 3	14.0 ± 0.5 [14.9] *n* = 3	210.7 ± 5.7 [243.0] *n* = 7	211.8 *n* = 1	172.0 ± 5.9 [182.0] *n* = 4	91.0 ± 3.4 [98.0] *n* = 4	49.0 ± 2.7 [55.0] *n* = 4	135.0 ± 34.0 [169.0] *n* = 2	28.8 ± 1.4 [29.2] *n* = 3

Variables: 1. Circumference of head at canine; 2. circumference of head at eye; 3. tip of snout to centre of eye; 4. tip of snout to centre of ear; 5. tip of snout to angle of gape; 6. standard body length; 7. ventral curvilinear length; 8. tip of snout to genital opening; 9. tip of snout to anterior insertion of the foreflipper; 10. length of foreflipper; 11. axillary girth; 12. length of hind flipper.

[a] Number of canine aged and known-age animals. Sample size given in square brackets where this does not equal total sample size.

[b] Mean value of variable ± S.E. for the 7 largest males (> 200 cm) of unknown-age; maximum value in square brackets, followed by sample size.

[c] V3 was poorly correlated with body variables and age (Appendix 3.2, 3.3 and 3.4), therefore had been excluded from further analysis.

[d] V7 was shown to be a poor indicator of SBL, therefore has been excluded from further analysis.

[e] V11 may be influenced by seasonal change and illness, therefore has been excluded from further analysis.

Table 3.4 *Growth in body variables (1–12) relative to the mean value of body measurement: (i) at age zero, RGR $\bar{y}_0$; and (ii) from the previous year, RGR $\bar{y}_{t-1}$*. All measurements are in cm.

Age group	**Age (y)**	***n*[a]**	**Var 1**	**Var 2**	**Var 4**	**Var 5**	**Var 6[b]**	**Var 8**	**Var 9**	**Var 10**	**Var 12**
Pup	< 1	3	–	–	–	–	–	–	–	–	–
Yearling	1	8	15.7; 15.7	16.1; 16.1 [7]	16.5; 16.5	7.1; 7.1	30.9; 30.9	36.5; 36.5	29.9; 29.9	27.1; 27.1	13.3; 13.3
Subadult	2	5	24.6; 7.7	28.0; 10.2	26.7; 8.8	9.2; 2.0	35.3; 3.4	43.2; 4.9	19.1; -8.3	33.6; 5.1	19.7; 5.7
	3	5	31.0; 5.1	33.7; 4.5	45.7; **15.0**	20.7; 10.5	62.7; **20.3**	76.4; **23.2**	54.3; **29.6**	55.8; 16.6	35.5; 13.2
	4	9	42.6; 8.9	42.7; 6.7	55.4; 6.6	38.1; 14.5	79.3; 10.2 [8]	92.7; 9.2 [8]	65.8; 7.4	71.2; 9.9	39.5; 3.0
	5	5	41.7; -0.6 [4]	44.6; 1.3 [4]	59.5; 2.6	20.9; -12.5 [3]	96.9; 9.8 [2]	124.0; 16.2	98.0; 19.4	103.0; 18.5	63.0; 16.8 [3]
	6	10	47.1; 3.8	54.3; 6.7	64.0; 2.8	42.3; 17.8 [9]	110.3; 6.8 [9]	127.8; 1.7	106.8; 4.5	90.9; -5.9 [9]	58.9; -2.5 [9]
	7	11	40.0; -4.9 [10]	44.3; -6.5 [10]	54.8; -5.7	29.9; -8.7	127.2; 8.1 [8]	138.3; 4.6	126.7; 9.6	97.3; 3.3	76.8; 11.3 [10]
Adult	8	6	42.8; 2.0 [5]	60.2; **11.0** [5]	61.0; 4.0	38.6; 6.7 [5]	132.2; 2.2 [3]	145.7; 3.1	142.0; 6.8	99.7; 1.2	95.1; **10.4**
	9	5	53.5; **7.5** [4]	55.2; -3.1	74.0; **8.1**	50.1; **8.3**	146.3; **6.1** [4]	174.5; **11.7**	164.6; **9.3**	130.5; **15.4**	111.4; 8.3
	10	4	57.3; 2.4 [3]	64.8; 6.2 [3]	69.9; -2.4	54.7; 3.1	163.7; **7.1**	186.4; 4.4	177.3; 4.8	128.7; -0.8	103.4; -3.7
	13	2	86.0; –	84.9; –	109.2; –	89.0; –	197.8; –	221.0; –	188.9; –	175.0; –	107.8; –
Total		**73**	**68**	**68**	**73**	**69**	**61**	**72**	**73**	**72**	**69**

Variables: 1. Circumference of head at canine; 2. circumference of head at eye; 4. tip of snout to centre of ear; 5. tip of snout to angle of gape; 6. standard body length (straight line from tip of snout to tip of tail); 8. tip of snout to genital opening. 9. tip of snout to anterior insertion of the foreflipper; 10. length of foreflipper (anterior insertion to tip of first claw); 11. axillary girth; and 12. length of hind flipper (anterior insertion to tip of first claw).

[a] Number of canine aged and known-age animals.

[b] For animals measured at sea (by-catch) it was not always possible to record SBL because of rough conditions, i.e., SBLs for 12 of these animals were not recorded.

Values for growth relative to age zero are presented on the left hand side of the relevant columns, i.e., $[(\bar{y}_t - \bar{y}_0)/\bar{y}_0] \times 100\%$. Values for growth relative to the previous year are presented on the right hand side of the relevant columns, i.e., $[(\bar{y}_t - \bar{y}_{t-1})/\bar{y}_{t-1}] \times 100\%$. Sample size given in square brackets where this does not equal total sample size.

Variables 3, 7 and 11 excluded from analysis (see footnotes in Table 3.3).

Mean SBL of males > 10 y, including unaged animals > 200 cm was 171.1 ± 3.4 cm ($n = 7$). Maximum recorded value was 184.0 cm (animal PEM2256, SBL 198 cm).

Tip of snout to anterior insertion of the foreflipper (V9)

Growth of tip of snout to anterior insertion of the foreflipper (V9) was rapid during the early postnatal period and continued to increase until at least 10 y (Table 3. 3 and 3.4). Overall growth expressed positive allometry relative to SBL, and negative allometry relative to age (Fig 3.3c; Appendix 3.3) (Fig 3.4c; Appendix 3.4). Growth increased by 177% at 10 y RTP (Table 3.4).

Mean SBL of males > 10 y, including unaged animals > 200 cm was 94.2 ± 3.1 cm ($n = 7$). Maximum recorded value was 110.0 cm (animal PEM2374, SBL 186 cm).

Length of foreflipper (V10)

Growth of length of foreflipper (V10) was rapid during the early postnatal period and continued to increased until at least 13 y (Table 3.3 and 3.4). A significant growth increment was evident between 4 and 5 y (two sample t test[1]: p-value = 0.015; df = 8). Overall growth scaled with negative slope relative to SBL ($b = 0.89$) and age ($b = 0.07$). Growth increased by 129% at 10 y RTP (Table 3.4). Growth increment decreased with increasing SBL until about 6 y (*c.* 23% of SBL) (Table 3.3).

Mean SBL of males > 10 y, including unaged animals > 200 cm was 47.2 ± 1.9 cm ($n = 8$). Maximum recorded value was 55.0 cm (animal PEM1560, SBL 201 cm).

Length of hind flipper (V12)

Growth of length of hind flipper (V12) was rapid during the early postnatal period and continued to increase until at least 8–9 y (Table 3.3 and 3.4). Overall growth scaled with negative slope relative to SBL ($b = 0.81$) and expressed negative allometry relative to age (Fig. 3.4d; Appendix 3.4), increasing by 103% at 10 y RTP (Table 3.4). Growth increment decreased with increasing SBL until about 4 y (*c.* 15% of SBL) (Table 3.3).

Mean SBL of males > 10 y, including unaged animals > 200 cm was 28.7 ± 0.9 cm ($n = 7$). Maximum recorded value was 32.0 cm (animal PEM1890, SBL 192 cm, ≥ 12 y).

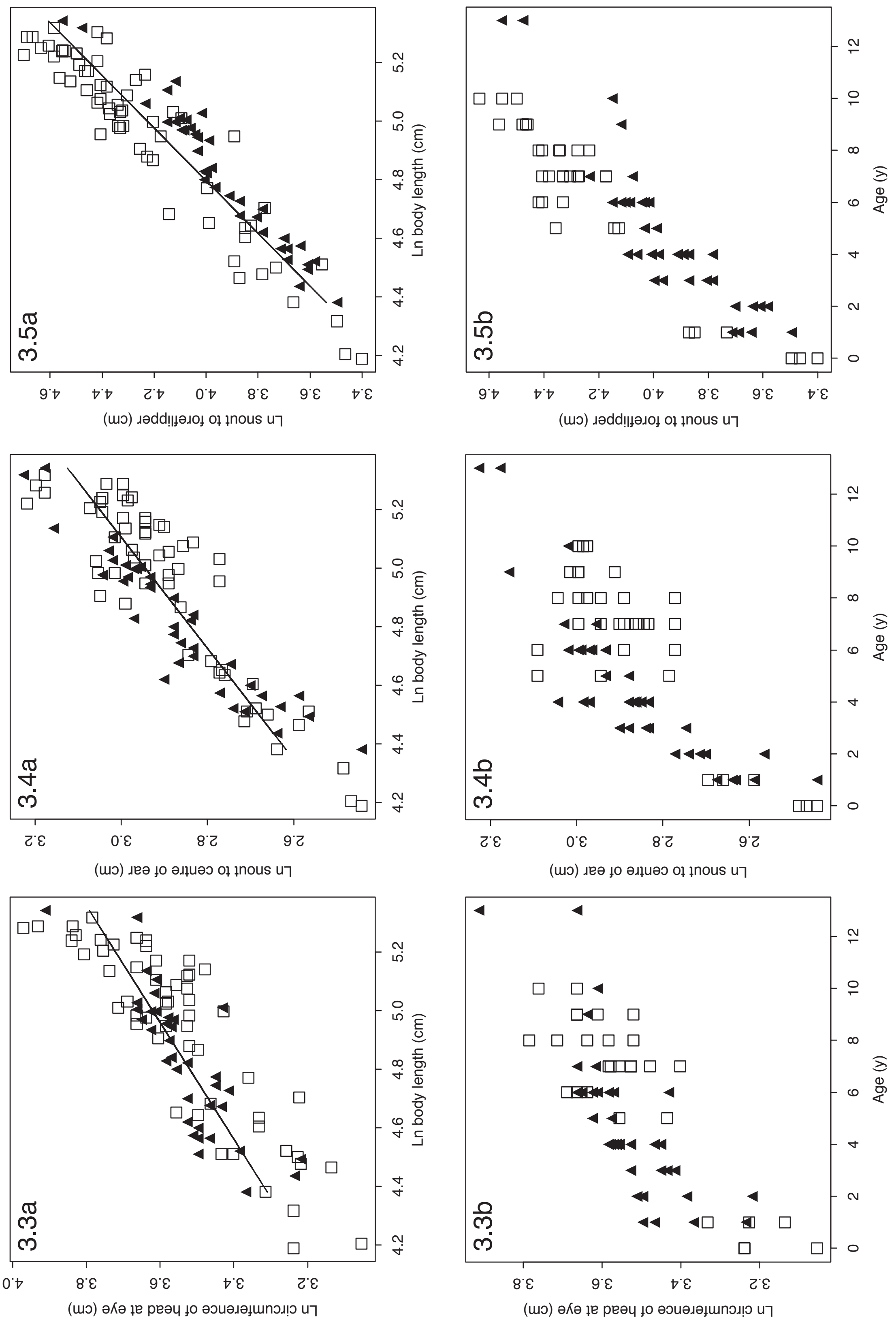
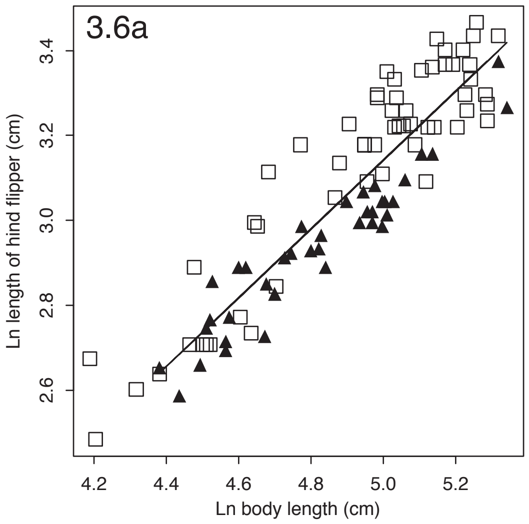
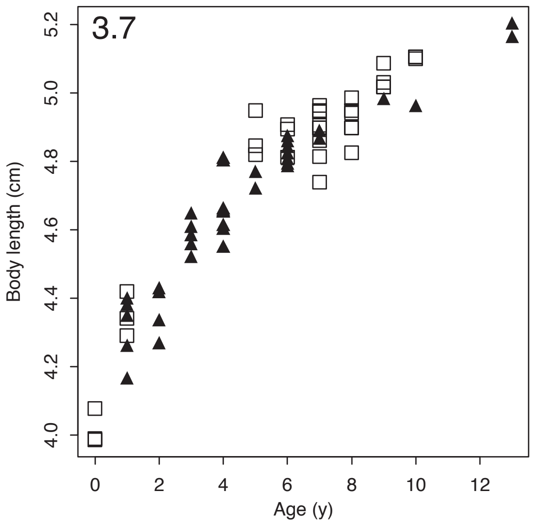


Fig. 3.3a, 3.3b Bivariate plot of log circumference of head at canine (cm) on: (a) log length of seal (cm) and (b) age (y).
Fig. 3.4a, 3.4b Bivariate plot of log tip of snout to centre of ear (cm) on: (a) log length of seal (cm) and (b) age (y).
Fig. 3.5a, 3.5b Bivariate plot of log tip of snout to anterior insertion of the foreflipper (cm) on: (a) log length of seal (cm) and (b) age (y).





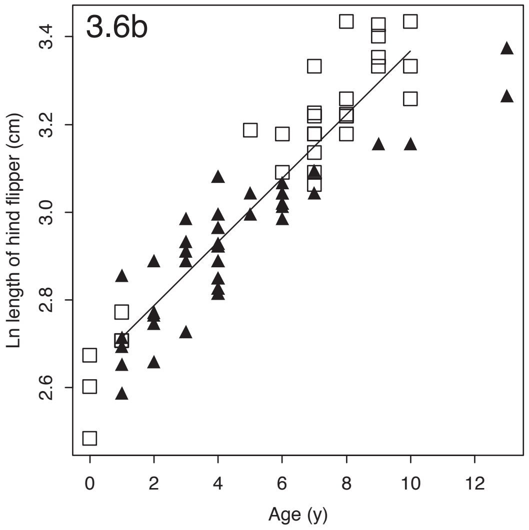


Fig. 3.6a, 3.6b Bivariate plot of log length of hind flipper (cm) on: (a) log length of seal (cm) and (b) age (y).
Fig. 3.7 Bivariate plot of log length of seal (cm) on age (y).

Body length as an indicator of age

In animals 1–10 y, growth in SBL was highly positively correlated with age (y) ($r = 0.96$, $n = 56$) (Appendix 3.4). After fitting the (robust) straight line model of age on standard body length, graphical displays of residuals and fitted values were examined, and the straight line model was found to be adequate. Thus, the following equation can be used as a very 'rough indicator' of absolute age for animals 1–10 y.

$$\text{age} = -6.54 + 0.0087 \times \text{SBL},\ n = 56$$

The coefficient of variation in SBL for young males 1–5 y (17.2%) was considerably higher than in older males (8–10 y, 6.9%; ≥ 12 y, 5.3%).

Body length as an indicator of age group

When SBL is known, the following linear discriminant functions can be used to categorise each observation into one of four age groups–pups, yearlings, subadults or subadult:

$$y_1 = -6.50 + 0.19x$$

$$y_2 = -11.14 + 0.25x$$

$$y_3 = -23.46 + 0.36x$$

$$y_4 = -45.28 + 0.50x$$

where x = SBL (cm); subscript 1 = pup; subscript 2 = yearling; superscript 3 = subadult; superscript 4 = adult. The seal is classified into the age group associated with the linear discriminant function which results in the minimum value. Of the 70 observations in this study 77% were correctly

Table 3.5 ***Discriminant analysis for seal age group (pup, yearling, subadult, adult) inferred from body length***

Known age group		**Classification into age group**			
		0	**1**	**2**	**3**
	n[a]	Pup (< 1 mo)	Yearling (7 mo to 1 y 6 mo)	Subadult (1y 7 mo to 7 y 6 mo)	Adult[b] (≥ 7 y 7 mo)
0	**3**	3 (100%)	1	0	0
1	**8**	0	7 (88%)	9	0
2	**37**	0	0	23 (62%)	1
3	**22**	0	0	5	21 (96%)
Total	**70**	**3**	**8**	**37**	**22**

[a] Number of seals of known-age (MCM animals tagged as pups), and aged from counts of incremental lines observed in the dentine of upper canines (PEM animals), $n = 70$. Percentage of animals correctly classified into age group is given in brackets.
[b] Included animals > 12 y.

classified using this method (Table 3.5).

Curvilinear length as an indicator of SBL

Curvelinear length was found to be approximately 10.0 cm longer than SBL (SBL: 146.7 ± 5.6; CBL: 157.1 ± 6.2, *n* = 50 paired samples only). However, CBL was greatly influenced by the quantity of food in the stomach and by the degree of postmortem bloating. For example, CBL was 20–25 cm longer than SBL in 5 animals that had been dead for several days, or had consumed large quantities of fish; therefore, CBL was not consider to be a useful substitute for SBL.

DISCUSSION

Age determination

Although the possibility of error must be taken into consideration when interpreting the data, age estimates were considered to be reliable, with inconsistencies among readings mitigated by repeated estimates (Doubleday & Bowen, 1980).

Body size

Arctocephalus pusillus is the largest of the fur seals. Male SBL ranged from 66 to 243 cm. The largest animal in the collection (PEM952) was measured in 1980 at Kings Beach, Port Elizabeth, by V. Cockcroft and A. Bachelor. This is of similar length to an unusually large male (SBL 241 cm) measured by Rand in 1946 (Rand, 1949). The largest animal measured by the first author was 203 cm in 1994 (PEM2201).

At birth, male Cape fur seals are about 35% (*c*. 69 cm) of their mean adult size[2] (*c*. 199.4 cm). At puberty they are about 57% (*c*. 112.8 cm at 3 y) of their mean adult size[2]. Although axillary girth varies with body condition, it is usually about 57–67% of SBL. The foreflippers are relatively long measuring 25–26% (*c*. 18 cm) of SBL in pups, and 24% (*c*. 48 cm) of SBL in adults[2]. The hind flippers are considerably shorter measuring 19% (*c*. 13 cm) of SBL in pups, and 14.5% (*c*. 29 cm) of SBL in adults[2].

Body shape

Male Cape fur seals are exceptional swimmers and divers, and haul out on land to rest, moult and breed. Body shape and general physiology have been modified to accommodate the demands of both marine and terrestrial environments (Bryden, 1972). For example, bulls spend most of their life at sea, hauling out to moult (predominantly February and March), rest, and reproduce (establish territories and breed from late October to late December/early January).

The body is streamlined with a rounded head and a relatively short snout; small external ear pinnae (narrow and pointed); a small tail positioned between the hind flippers; a retractable penis that can be withdrawn into a cutaneous pouch; and modified fore/hind limbs (flippers).

The strong fore limbs have been modified into elongated flippers for propulsion through the water (forceful strokes towards the body) and terrestrial locomotion (palm extends laterally with the flipper bending between the two rows of carpal bones). Characteristic features include predigital cartilage, a long first digit, reduced fifth digit, rudimentary nails and hairless palms.

Unlike the foreflippers which are the primary appendage used for propulsion through the water, the smaller hind flippers have been modified for terrestrial locomotion (soles extends laterally with the flipper bending forward at the ankle). Characteristic features include predigital cartilage; long grooming claws on digits 2–4; enlargement of digits one and five; and hairless soles.

Function and growth

Overall growth in SBL was similar to that of other highly polygynous male otariids including *A. gazella* and *C. ursinus*, with rapid early postnatal growth; a sudden increase in body size at puberty; and a reduced rate of growth soon after attainment of social maturity (McLaren, 1993).

Cape fur seals pups are born on land between October to late December. New born pups are *c*. 35% (60–70 cm at birth) of mean adult size. During the first week, pups are largely inactive. As they become older, they gradually learn swimming skills in pools and sheltered channels. Growth during this period is rapid (present study), with males growing faster than females. For example, in November (when the majority of pups are born), mean length and weight is about 76 .0 cm and 5 kg 986 g for males, and 73 cm and 5 kg 487 g for females (Rand, 1956). By April, mean length and weight is about 82 .0 cm and 19 kg 183 g for males, and 84 cm and 15 kg 147 g for females (Rand, 1956).

When juveniles gain their permanent teeth (June) they disperse to deeper water for short periods, supplementing their milk diet with solids (Rand, 1956). During this period they learn foraging skills while accompanying their lactating mothers to sea. Most animals feed independently at 9–11 mo (Rand, 1956). There is a decline in body weight soon after weaning (Rand, 1956).

Most males attain puberty between 3–4 y, with sperm evident in the epididymis of some animals at 2 y 10 m (Stewardson *et al.*, 1998). The onset of puberty (2–3 y) is associated with a sudden increase in body size (present study). It is thought that puberty is attained when mammals reach a certain threshold size in body weight, with slower-growing animals

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[2] Mean adult size, SBL for animals > 10 y including unaged animals > 200 cm.

reaching puberty later than faster-growing animals (Laws & Sinha, 1993). Although pubertal males produce sperm, they do not have the ability to acquire and maintain a harem. Small body size and inexperience prevents young males form gaining high social status.

Growth in SBL continues to increase steadily until about 6 y. In animals ≥ 7 y, growth continues to increase but at a slower rate (present study).

Social maturity is attained at about 9–10 y and appears to be associated with a weak secondary growth spurt in body size (present study). At this age, large body size has a direct advantage in competitive interactions with rival males, and an indirect effect through the presence of large stores of fat which enable males to remain on territory for up to 40 days (Rand, 1967; Wartzok, 1991). Successful bulls may mate multiple times over a two to three year period and are likely to die before reaching reproductive senescence (see Stewardson *et al.,* 1998). Growth in body size slows soon after attainment of social maturity (present study).

Growth of length of the foreflippers continued to increased until at least 13 y, with a significant increase in length at 4–5 y (present study). This increase may partially reflect changes in swimming and/or diving behaviour, with older animals presumably diving to deeper depths in search of prey. Growth of the smaller hind flippers slowed much earlier (8–9 y) than growth of the foreflippers. No special development of the foreflippers or hind flippers associated with locomotion was reported in *A. gazella*, i.e., a more or less constant rate of growth from age one to 7 (Payne, 1979).

Body length as an indicator of age

SBL could not be used reliably to assign a seal to a particular age because there was considerable overlap between year classes, especially among older animals. Similar findings have been reported in other species of pinnipeds (e.g., Laws, 1953; Bryden 1972; Bengtson & Sniff, 1981). However, SBL was found to be a 'very rough indicator' of age for animals 1–10 y, and of age group.

The classification criteria for age and age group developed in this study will be particularly useful when canines are not available for age determination, e.g. behavioural studies.

CONCLUSION

Information presented in this study contributes to earlier descriptions of the Cape fur seal (Rand, 1956), and provides new information on body growth according to age (y).

In male Cape fur seals, post natal growth is rapid with a significant growth spurt at at the onset of puberty (2–3 y) and a weak growth spurt at social maturity (9–10 y). Growth continues to increase but at a slower rate between 6 and 7 y, and then slows soon after the attainment of social maturity. Growth was a differential process and not simply an enlargement of overall size. Relative to SBL, facial variables and the fore/hind limbs scaled with negative slope relative to SBL or were negatively allometric; tip of snout to genital opening scaled with positive slope; and tip of snout to anterior insertion of the foreflipper was positively allometric. Relative to age, body variables scaled with negative slope or were negatively allometric. SBL was found to be a 'very rough indicator' of age and of age group.

Further information is needed on animals of known-age in order to accurately estimate asymptotic size. In the present study, low sample size at the intermediate ages, and the absence of very old animals of known-age (18–20 y), made it difficult to determine the exact shape of the growth curve. Furthermore, information on the breeding status of known-age males is required. Breeding bulls are thought to be larger in size than non-breeding bulls of the same age, therefore, the observed growth pattern is more complex than is presented in this study.

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Appendix 3.1 ***Cape fur seals (n = 149) examined in this study.*** **Animals were collected from the coast of southern Africa between August 1978 and September 1997.**

	ID No.	Date of collection	Approximate location[b]	Region[c]	Method of collection[d]	SBL (cm)
1.	PEM603	2 Aug 78	Bell Buoy, Algoa Bay (AB) (33º 59’S, 25º 42’E)	ECP	sci. permit	150
2.	PEM605	4 Apr 79	Riy Bank, AB (34º 00’S, 25º 53’E)	ECP	sci. permit	153
3.	PEM607	30 Sep 79	King’s Beach, Port Elizabeth (PE) (33º 58’S, 25º 39’E)	ECP	rehab. (D)	91
4.	PEM608	29 Aug 79	Cape Recife–Riy Bank, AB (34º 02’S, 25º 42’E– 34º 00’S, 25º 53’E)	ECP	sci. permit	182
5.	PEM658	17 July 80	2 km E Kabeljous River Mouth, Jeffreys Bay	ECP	stranding	106
6.	PEM661	17 July 74	Riy Bank–St. Croix, AB (34º 00’S, 25º 53’E– 33º 48’S, 25º 46’E)	ECP	sci. permit	141
7.	PEM670	5 Mar 79	King’s Beach, PE (33º 58’S, 25º 39’E)	ECP	stranding	158
8.	PEM676	16 Feb 81	NR	ECP	oceanarium	197
9.	PEM824	23 Mar 82	Pollock Beach, PE (33º 59’20”S, 25º 40’ 30”E)	ECP	stranding	174
10.	PEM828	26 Mar 82	Port Elizabeth Harbour (33º 58’S, 25º 37’E)	ECP	stranding	158
11.	PEM834	21 Apr 82	22 km E of Sundays River Mouth, Woody Cape (WC)	ECP	stranding	162
12.	PEM852	21 July 82	15 km E Sundays River Mouth, WC	ECP	stranding	195
13.	PEM874	18 Oct 82	32 km E of Sundays River Mouth, WC	ECP	stranding	157
14.	PEM875	20 Sep 82	1 km W of Van Starden’s River Mouth	ECP	stranding	165
15.	PEM877	2 Oct 82	E of Swartkops River Mouth, AB	ECP	stranding	165
16.	PEM886	23 Oct 82	Pollock Beach, PE (33º 59’20”S, 25º 40’ 30”E)	ECP	stranding	193
17.	PEM888	2 Nov 82	7 km E of Kasuga River Mouth, Port Alfred (PA)	ECP	stranding	212
18.	PEM889	2 Nov 82	4 km E of Kasuga River Mouth, PA	ECP	stranding	138
19.	PEM898	22 Dec 82	1 km E of Van Starden’s River Mouth, St. Francis Bay (FB)	ECP	stranding	200
20.	PEM916	Jan 1983	Willows, PE (34º 03’S, 25º 35’E)	ECP	stranding	91
21.	PEM917	11 Jan 83	2 km W of Maitland River Mouth, FB	ECP	stranding	104
22.	PEM928	14 Mar 82	28 km E of Sundays River Mouth, WC	ECP	stranding	140
23.	PEM951	16 May 83	35 km E of Sundays River Mouth, WC	ECP	stranding	170
24.	PEM952[a]	22 Feb 80	King’s Beach, PE (33º 58’S, 25º 39’E)	ECP	stranding	243
25.	PEM958	13 Dec 83	Humewood, PE (33º 59’S, 25º 40’E)	ECP	other	190
26	PEM975	7 Oct 83	40 km E of Sundays River Mouth, WC	ECP	stranding	172
27.	PEM1073	12 Sep 84	Oyster Bay (34º 10’S, 24º 39’E)	ECP	stranding	133
28.	PEM1135	6 Feb 85	15 km E Sundays River Mouth, WC	ECP	stranding	141
29.	PEM1159	20 May 85	3.5 km W of Woody Cape Point	ECP	stranding	190
30.	PEM1453	30 Jan 88	3 km E Kabeljous River Mouth, Jeffreys Bay	ECP	stranding	193
31.	PEM1507	5 Feb 88	King’s Beach, PE (33º 58’S, 25º 39’E)	ECP	stranding	198
32.	PEM1560	26 Oct 88	Seaview (34º 01’E, 25º 17’S)	ECP	stranding	201
33.	PEM1587	18 May 89	Amsterdamhoek (33º 52’S, 25º 38’E)	ECP	stranding	192
34.	PEM1696	12 Apr 90	5 km E of Sundays River Mouth, WC	ECP	stranding	202
35.	PEM1697	12 Apr 90	15 km E of Sundays River Mouth, WC	ECP	stranding	192
36.	PEM1698	12 Apr 90	25 km E of Sundays River Mouth, WC	ECP	stranding	190
37.	PEM1706	12 July 90	1.5 km E of Sundays River Mouth, WC	ECP	stranding	126
38.	PEM1879	13 Apr 92	Flat Rocks, PE (34º 00’S, 25º 42’E)	ECP	stranding	200
39.	PEM1882	6 May 92	King’s Beach, PE (33º 58’S, 25º 39’E)	ECP	stranding	180
40.	PEM1885	17 June 92	1 km W of Cape Recife, PE	ECP	stranding	80
41.	PEM1890	13 July 92	Cape Recife, PE (34º 02’S, 25º 42’E)	ECP	stranding	192
42.	PEM1892	27 July 92	Sardinia Bay (34º 02’S, 25º 29’E), 800 m E of boat shed	ECP	stranding	185
43.	PEM1895	29 July 92	Cape Recife, PE (34º 02’S, 25º 42’E), 2 km E of lighthouse	ECP	stranding	188
44.	PEM1999	20 July 92	EC trawl grounds (34º 52’S, 23º 35’E–34º 50’S, 23º 48’E)	ECP	by-catch	–
45.	PEM2000	21 July 92	EC trawl grounds (34º 50’S, 23º 48’E–34º 48’S, 24º 00’E)	ECP	by-catch	–
46.	PEM2002	22 July 92	EC trawl grounds (34º 55’S, 23º 14’E–34º 53’S, 23º 26’E)	ECP	by-catch	–
47.	PEM2003	24 July 92	EC trawl grounds (34º 51’S, 23º 42’E–34º 49’S, 23º 53’E)	ECP	by-catch	–
48.	PEM2004	25 July 92	EC trawl grounds (34º 45’S, 24º 18’E–34º 48’S, 24º 00’E)	ECP	by-catch	–
49.	PEM2006	13 Aug 92	EC trawl grounds (34º 45’S, 24º 25’E–34º 42’S, 24º 40’E)	ECP	by-catch	–
50.	PEM2007	14 Aug 92	EC trawl grounds (34º 42’S, 24º 51’E–34º 42’S, 24º 42’E)	ECP	by-catch	–
51.	PEM2008	14 Aug 92	EC trawl grounds (34º 41’S, 24º 42’E–34º 38’S, 24º 54’E)	ECP	by-catch	–
52.	PEM2009	22 Aug 92	EC trawl grounds (34º 41’S, 24º 45’E–34º 37’S, 24º 59’E)	ECP	by-catch	–
53.	PEM2010	22 Aug 92	EC trawl grounds (34º 47’S, 24º 11’E–34º 46’S, 24º 25’E)	ECP	by-catch	–
54.	PEM2013	14 Sep 92	EC trawl grounds (34º 24’S, 25º 50’E–34º 25’S, 26º 02’E)	ECP	by-catch	–
55.	PEM2014	25 Sep 92	EC trawl grounds (34º 23’S, 26º 04’E–34º 23’S, 25º 58’E)	ECP	by-catch	–
56.	PEM2015	3 Nov 92	EC trawl grounds (34º 17’S, 24º 36’E–34º 20’S, 24º 23’E)	ECP	by-catch	–
57.	PEM2020	28 Jan 93	Kenton-on-sea (33º 40’S, 26º 40’E)	ECP	euthanased	66
58.	PEM2021	28 Jan 93	Swartkops River Mouth	ECP	stranding	75
59.	PEM2036	19 Mar 93	Black Rocks, AB (33° 50’S, 26° 15’E)	ECP	stranding	–

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	ID No.	Date of collection	Approximate location[b]	Region[c]	Method of collection[d]	SBL (cm)
60.	PEM2045	30 May 93	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	145
61.	PEM2046	19 May 93	EC trawl grounds (35° 09'S, 21° 28'E)	ECP	by-catch	141
62.	PEM2047	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	ECP	by-catch	167
63.	PEM2048	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	ECP	by-catch	157
64.	PEM2049	7 June 93	Kini Bay (34° 01'S, 25° 26'E), Western Beach	ECP	stranding	174
65.	PEM2051	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	ECP	by-catch	168
66.	PEM2052	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	ECP	by-catch	171
67.	PEM2053	28 June 93	EC trawl grounds (34° 46'S, 24° 21'E–34° 44'S, 24° 32'E)	ECP	by-catch	153
68.	PEM2054	29 June 93	EC trawl grounds (34° 45'S, 24° 28'E–34° 47'S, 24° 18'E)	ECP	by-catch	165
69.	PEM2081	19 July 93	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	162
70.	PEM2082	July 93	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	176
71.	PEM2087	17 Aug 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	ECP	stranding	190
72.	PEM2131	13 Dec 93	Sundays River Mouth, AB	ECP	rehab. (D)	67
73.	PEM2132	20 Dec 93	Woody Cape, AB (33° 46'S, 26° 19'E)	ECP	stranding	195
74.	PEM2137	5 Jan 94	Summerstrand, PE (34° 00'S, 25° 42'E)	ECP	rehab. (D)	118
75.	PEM2140	17 Jan 94	40 km E of Sundays River Mouth, WC	ECP	stranding	187
76.	PEM2141	17 Jan 94	39 km E of Sundays River Mouth, WC	ECP	stranding	198
77.	PEM2143	21 Jan 94	Seaview (34° 01'S, 25° 17'E)	ECP	stranding	189
78.	PEM2186	7 Apr 94	Amsterdamhoek (33° 52'S, 25° 38'E)	ECP	rehab. (D)	90
79.	PEM2188	17 Apr 94	NR	ECP	oceanarium	132
80.	PEM2191	4 May 94	Port Alfred (33° 36'S, 26° 55'E)	ECP	euthanased	100
81.	PEM2194	2 June 94	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	194
82.	PEM2197	12 July 94	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	160
83.	PEM2198	July 94	Plettenberg Bay (34° 03'S, 23° 24'E)	ECP	stranding	105
84.	PEM2201	5 July 94	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	103
85.	PEM2203	18 July 94	Port Elizabeth Harbour (33° 58'S, 25° 37'E)	ECP	other	204
86.	PEM2238[e]	1994	Durban (29° 50'S, 31° 00'E)	ECP	rehab. (D)	96
87.	PEM2248	12 Aug 94	Seaview (34° 01'S, 25° 27'E)	ECP	stranding	158
88.	PEM2252	22 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	172
89.	PEM2253	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	152
90.	PEM2254	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	146
91.	PEM2256	17 Sep 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	198
92.	PEM2257A	19 Sep 94	EC trawl grounds	ECP	by-catch	142
93.	PEM2257B	8 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	170
94.	PEM2348	14 Nov 94	Humewood, PE (33° 59'S, 25° 40'E)	ECP	stranding	189
95.	PEM2359	21 Feb 95	Sundays River Mouth, AB	ECP	stranding	108
96.	PEM2374	24 Mar 95	Jeffreys Bay (34° 03'S, 24° 55'E)	ECP	stranding	186
97.	PEM2379	12 Apr 95	Bokness (33° 41'S, 26° 31'E)	ECP	stranding	189
98.	PEM2400	13 July 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	176
99.	PEM2401	13 July 95	EC trawl grounds	ECP	by-catch	146
100.	PEM2403	July 95	NR	ECP	rehab. (D)	88
101.	PEM2404	July 95	NR	ECP	rehab. (D)	92
102.	PEM2405	July 95	NR	ECP	rehab. (D)	87
103.	PEM2406	July 95	Swartkops River Mouth	ECP	stranding	154
104.	PEM2409	24 Aug	Oceanarium animal (Muti)	ECP	oceanarium	135
105.	PEM2411	24 Aug 95	Plettenberg Bay (34° 03'S, 23° 24'E)	ECP	by-catch	155
106.	PEM2414	25 Aug 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	148
107.	PEM2415	27 Aug 95	Sardinia Bay (34° 02'S, 25° 29'E)	ECP	stranding	130
108.	PEM2454	8 Nov 95	Noordhoek (34° 02'S, 25° 39'E)	ECP	stranding	196
109.	PEM2455	27 Nov 95	2.3 km W of Maitland River Mouth, FB	ECP	stranding	124
110.	PEM2458	3 Dec 95	Cape St. Francis (34° 12'S, 24° 52'E)	ECP	rehab. (D)	110
111.	MCM1565	25 Sep 84	Vondeling area (33° 18'S, 18° 06'E), 2 miles offshore	WC	sci. permit	118
112.	MCM1786	30 Sep 94	St Helena Bay	WC	stranding	85
113.	MCM2763	10 Feb 85	Doringbaai area (31° 30'S, 16° 30'E)	WC	by-catch	127
114.	MCM2795	27 July 88	Demersal fishing grid 502	SWC	by-catch	158
115.	MCM3017	14 Nov 85	Kleinzee seal colony	WC	sci. permit	209
116.	MCM3125	17 Nov 85	Kleinzee seal colony	WC	sci. permit	204
117.	MCM3582	6 June 86	Offshore Dassen Island (33° 21'S, 17° 40'E)	WC	by-catch	142
118.	MCM3586	22 Apr 86	8 miles off Wilderness	SC	by-catch	144
119.	MCM3587	5 June 86	25 nm west of Mossel Bay	SC	by-catch	145

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	ID No.	Date of collection	Approximate location[b]	Region[c]	Method of collection[d]	SBL (cm)
120.	PEM3589	8 Dec 86	West of Slangkop	WC	by-catch	148
121.	MCM3636	17 July 87	West of Dassen Island (37° 45'S, 17° 35'E)	WC	by-catch	148
122.	MCM4023	28 June 89	St Helena Bay (32° 30'S, 18° 16'E)	WC	sci. permit	113
123.	MCM4365	13 Mar 90	3.5 nm off Gouritz River Mouth (34° 23'S, 21° 51'E)	SC	by-catch	124
124.	MCM4388	23 Oct 90	20 nm south of Gouritz River Mouth (34° 26'S, 21° 53'E)	SC	by-catch	122
125.	MCM4577	17 Jan 94	Cape Town Harbour	WC	stranding	150
126.	MCM4584	19 Jan 95	St Helena Bay (32° 44'S, 18° 08'E)	WC	by-catch	125
127.	MCM4585	19 Jan 95	St Helena Bay (32° 44'S, 18° 08'E)	WC	by-catch	–
128.	MCM4595	17 Oct 95	Off Cape Point (34° 45'S, 21° 49'E)	SW	by-catch	134
129.	MCM4597	15 Sep 95	South of Dassen Island (33° 30'S, 17° 40'E)	WC	by-catch	170
130.	MCM4985	26 June 96	1 nm off Sandy Point harbour	WC	by-catch	92
131.	MCM4987	8 May 96	Offshore Hut Bay (34° 16'S, 17° 43'E)	WC	by-caych	144
132.	MCM4989	14 Aug 96	St Helena Bay	WC	by-catch	99
133.	MCM4991	15 Aug 96	St Helena Bay	WC	by-catch	102
134.	MCM4992	13 Sep 96	Demersal fishing grid 493 (35° 30'S, 18° 56'E)	SW	by-catch	165
135.	MCM4996	28 Sep 96	Offshore Saldahna Bay (33° 10'S, 17° 14'E)	WC	by-catch	115
136.	MCM4998	10 July 96	Seal Island, St Helena Bay	WC	by-catch	93
137.	MCM4999	10 July 96	Seal Island, St Helena Bay	WC	by-catch	80
138.	MCM5000	10 Jan 96	Seal Island, St Helena Bay	WC	by-catch	96
139.	MCM5001	10 Jan 96	Seal Island, St Helena Bay	WC	by-catch	96
140.	MCM5002	10 June 96	Offshore Saldahna Bay (33° 16'S, 17° 07'E)	WC	by-catch	108
141.	MCM5005	18 Oct 96	Off Paternoster Island	WC	by-catch	91
142.	MCM5021	26 Dec 96	Offshore Saldahna Bay (33° 12'S, 17° 13'E)	WC	by-catch	141
143.	MCM5022	26 Nov 96	18 nm East of Mossel Bay (34° 25'S, 25° 50'E)	SC	by-catch	139
144.	MCM5133	14 Jan 97	Offshore Plettenberg Bay (34° 30'S, 23° 30'E)	ECP	by-catch	153
145.	MCM5134	22 May 97	8 nm off Shelly Point, St Helena Bay	WC	by-catch	97
146.	MCM5135	23 July 97	Offshore Stompneus Lighthouse	WC	stranding	110
147.	MCM5136	15 July 97	Offshore St Helena Bay (32° 27'S, 17° 38'E)	WC	by-catch	149
148.	MCM5142	19 Aug 97	Vondeling Island	WC	by-catch	107
149.	MCM5145	Nov 94	St Helena Bay	WC	by-catch	90

[a] Animal collected in 1980 and issued with a new identification number in 1983, i.e., PEM952.

[b] Kabeljous River Mouth (34° 00'S, 24° 56'E); Maitland River Mouth (33° 59'S, 25° 18'E); Sundays River Mouth (33° 43'S, 25° 51'E); and Van Starden's River Mouth (33° 58'S, 25° 13'E).

[c] WC (west coast), north of Cape Point Lighthouse (34° 21'S, 18° 29'E); SWC (south west coast), south of Cape Point Lighthouse to Cape Agulhas (34° 50'S, 20° 00'E); SC (south coast), east of Cape Agulhas, but excluding the Eastern Cape; and ECP (Eastern Cape Province), Plettenberg Bay (34° 03'S, 23° 24'E) to East London (33° 03'S, 27° 54'E).

[d] Stranding, animal washed up dead on beach ($n = 62$). By-catch, animal incidentally caught in a commercial trawl net during fishing operations ($n = 63$). Rehab. (D), animal died during rehabilitation at the Port Elizabeth Oceanarium ($n = 9$). Euthanased, animal suffering from illness/injury and was put down to prevent further suffering ($n = 2$). Sci. permit, animal collected under scientific permit or harvested (n = 8). Oceanarium, captive animal of the Port Elizabeth Oceanarium ($n = 3$, PEM676 Tommy; PEM2188 Rascal; PEM2409 Muti). Other, animal died from other causes ($n = 2$, PEM958 found floating in the ocean off Humewood Beach; PEM2203 stoned to death by fisherman).

[e] Animal PEM2238 collected NE of the Eastern Cape, i.e., Durban (29° 50'S, 31° 00'E).

NR, not recorded.

Appendix 3.2 _Spearman rank-order correlation coefficients for log body variables_

	Var 1	**Var 2**	**Var 3**	**Var 4**	**Var 5**	**Var 6**	**Var 7**	**Var 8**	**Var 9**	**Var 10**	**Var 11**	**Var 12**
Var 1	1.00 (99)	0.82* (98)	_0.12_ [0.27] (85)	0.74* (97)	0.63* (94)	0.77* (87)	0.84* (54)	0.76* (96)	0.71* (98)	0.71* (96)	0.82* (81)	0.72* (93)
Var 2	0.82* (98)	1.00 (102)	_0.17_ [0.11] (87)	0.76* (100)	0.61* (97)	0.62* (90)	0.81* (57)	0.78* (97)	0.73* (101)	0.74* (99)	0.86* (83)	0.72* (96)
Var 3	_0.12_ [0.27] (85)	_0.17_ [0.11] (87)	1.00 (101)	_0.25_** [0.02] (93)	_0.25_** [0.02] (89)	_0.15_ [0.17] (87)	_0.002_ [0.99] (54)	_0.08_ [0.46] (90)	_0.17_ [0.10] (92)	_0.12_ [0.26] (90)	_0.07_ [0.54] (71)	_0.15_ [0.16] (87)
Var 4	0.74* (97)	0.76* (100)	_0.25_** [0.02] (93)	1.00 (108)	0.85* (104)	0.84* (93)	0.68* (61)	0.79* (103)	0.74* (106)	0.85* (104)	0.79* (85)	0.76* (101)
Var 5	0.63* (94)	0.61* (97)	_0.25_** [0.02] (89)	0.85* (104)	1.00 (105)	0.78* (94)	0.68* (57)	0.69* (100)	0.68* (103)	0.72* (102)	0.71* (86)	0.68* (101)
Var 6	0.77* (87)	0.82* (90)	_0.15_ [0.17] (87)	0.84* (93)	0.78* (94)	1.00 (131)	0.96* (51)	0.99* (94)	0.93* (95)	0.92* (93)	0.94* (86)	0.90* (92)
Var 7	0.84* (54)	0.81* (57)	_0.002_ (54)	0.68* (61)	0.68* (57)	0.96* (51)	1.00 (65)	0.97* (60)	0.92* (61)	0.74* (59)	0.92* (45)	0.82* (57)
Var 8	0.76* (96)	0.78* (97)	_0.08_ [0.46] (90)	0.79* (103)	0.69* (100)	0.99* (94)	0.97* (60)	1.00 (107)	0.93* (104)	0.89* (102)	0.94* (84)	0.90* (99)
Var 9	0.71* (98)	0.73* (101)	_0.17_ [0.10] (92)	0.74* (106)	0.68* (103)	0.93* (95)	0.92* (61)	0.93* (104)	1.00 (109)	0.82* (105)	0.89* (87)	0.91* (102)
Var 10	0.71* (96)	0.74* (99)	_0.12_ [0.26] (90)	0.85* (104)	0.72* (102)	0.92* (93)	0.74* (59)	0.89* (102)	0.82* (105)	1.00 (107)	0.88* (85)	0.87* (101)
Var 11	0.82* (81)	0.86* (83)	_0.07_ [0.54] (71)	0.79* (85)	0.71* (86)	0.94* (86)	0.92* (45)	0.94* (84)	0.89* (87)	0.88* (85)	1.00 (87)	0.85* (86)
Var 12	0.72* (93)	0.72* (96)	_0.15_ [0.16] (87)	0.76* (101)	0.68* (101)	0.90* (92)	0.82* (57)	0.90* (99)	0.91* (102)	0.87* (101)	0.85* (86)	1.00 (103)
Total	**99**	**102**	**101**	**108**	**105**	**131**	**65**	**107**	**109**	**107**	**87**	**103**

Variables: 1. Circumference of head at canine; 2. circumference of head at eye; 3. tip of snout to centre of eye; 4. tip of snout to centre of ear; 5. tip of snout to angle of gape; 6. standard body length; 7. ventral curvilinear length; 8. tip of snout to genital opening; 9. tip of snout to anterior insertion of the foreflipper; 10. length of foreflipper; 11. axillary girth; and 12. length of hind flipper.

Pups excluded from analysis.

p = 0.00 unless otherwise stated in square brackets.

* Significant at 2% level (2-tailed).

** Significant at 1% (2-tailed).

Sample size in round brackets.

Appendix 3.3 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log body measurement (cm) on log seal body length (cm)***

Dependent variable	**Linear regression**				**Allometry**		
	n^a	**Intercept ± S.E.**	**Slope ± S.E.**	***r*** **(*p*)**	**Alternative hypothesis**	***d.f.***	***p***
1. Circumference of head at canine	87	0.89 ± 0.18	0.47 ± 0.04	0.77 (0.00)	$H_1 : \hat{\beta} < 1$	85	0.00
2. Circumference of head at eye	90	1.09 ± 0.18	0.50 ± 0.04	0.82 (0.00)	$H_1 : \hat{\beta} < 1$	88	0.00
3. Tip of snout to centre of eye[b]	87	–	–	0.15 (0.16)	–	–	–
4. Tip of snout to centre of ear	93	0.30 ± 0.14	0.53 ± 0.03	0.84 (0.00)	$H_1 : \hat{\beta} < 1$	91	0.00
5. Tip of snout to angle of gape	94	-0.82 ± 0.22	0.64 ± 0.04	0.78 (0.00)	NA	NA	NA
8. Tip of snout to genital opening	94	-0.35 ± 0.07	1.04 ± 0.01	0.99 (0.00)	NA	NA	NA
9. Tip of snout to anterior insertion of the foreflipper	95	-1.33 ± 0.22	1.11 ± 0.05	0.93 (0.00)	$H_1 : \hat{\beta} > 1$	93	0.007
10. Length of foreflipper	93	-0.91 ± 0.18	0.89 ± 0.04	0.92 (0.00)	NA	NA	NA
12. Length of hind flipper	92	-0.91 ± 0.19	0.81 ± 0.04	0.90 (0.00)	NA	NA	NA
Total	**116**						

[a] Number of aged and unaged animals with SBL recorded (pups were excluded from analysis, and SBLs from 15 aged/unaged males were not recorded, i.e., $n = 116$).

r, Spearman rank-order correlation coefficient.

All correlations are significant at the 1% level (2-tailed) apart from V3.

NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.

[b] Model assumptions met; however, linear regression not significant.

Variables 7 and 11 excluded from analysis (see footnotes in Table 3.3).

Appendix 3.4 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log body measurement (cm) on age (y)***

Dependent variable	**Linear regression**				**Allometry**		
	n^a	**Intercept ± S.E.**	**Slope ± S.E.**	***r*** **(*p*)**	**Alternative hypothesis**	***d.f.***	***p***
1. Circumference of head at canine	63	-2.59 ± 0.50	0.17 ± 0.021	0.59 (0.00)	$H_1 : \hat{\beta} < 1$	61	0.00
2. Circumference of head at eye	63	-2.63 ± 0.43	0.12 ± 0.01	0.69 (0.00)	NA	NA	NA
3. Tip of snout to centre of eye[b]	57	–	–	-0.008 (0.95)	–	–	–
4. Tip of snout to centre of ear	68	2.67 ± 0.02	0.04 ± 0.004	0.69 (0.00)	NA	NA	NA
5. Tip of snout to angle of gape	64	2.03 ± 0.03	0.04 ± 0.005	0.56 (0.00)	$H_1 : \hat{\beta} < 1$	62	0.00
6. Standard body length	56	4.45 ± 0.02	0.08 ± 0.003	0.96 (0.00)	NA	NA	NA
8. Tip of snout to genital opening	67	-1.28 ± 0.14	0.02 ± 0.001	0.93 (0.00)	NA	NA	NA
9. Tip of snout to anterior insertion of the foreflipper	68	3.56 ± 0.03	0.10 ± 0.005	0.90 (0.00)	$H_1 : \hat{\beta} < 1$	66	0.00
10. Length of foreflipper	67	3.10 ± 0.03	0.07 ± 0.005	0.82 (0.00)	NA	NA	NA
12. Length of hind flipper	64	2.64 ± 0.02	0.07 ± 0.004	0.93 (0.00)	$H_1 : \hat{\beta} < 1$	62	0.00
Total	**68**						

[a] Number of skulls with body variable and age recorded (only animals 1–10 y were included in analysis, i.e., $n = 68$).

r, Spearman rank-order correlation coefficient.

All correlations are significant at the 1% level (2-tailed), except for V3.

NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.

[b] Model assumptions met; however, linear regression not significant.

Variables 7 and 11 excluded form analysis (see footnotes in Table 3.3).

CHAPTER 4

Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part two, skull

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ABSTRACT

Morphology, relative size and growth of the skull in 83 Cape fur seals, *Arctocephalus pusillus pusillus*, from the coast of southern Africa are described. Skull measurements ($n = 32$ variables) were examined in relation to standard body length (SBL), condylobasal length (CBL) and chronological age (y) using linear regression. Animals ranged from 10 mo to ≥ 12 y. Twenty four animals were of known-age, while 39 were aged from counts of incremental lines observed in the dentine of tooth sections. Morphological observations were generally consistent with earlier studies by Rand (1949*b*, 1950, 1956) and Repenning *et. al.*, (1971). Condylobasal length was highly, positively correlated with SBL and age. Overall, skull variables grew at a slower rate than SBL, apart from height of mandible at meatus and angularis to coronoideus, which expressed isometry relative to SBL. Condylobasal length continued to increase until at least 12 y, with no obvious growth spurt between 8–10 y, when social maturity (full reproductive capacity) is attained. Mean CBL was 19.4% of SBL in yearlings; 15.5% in subadults, and 13.7% in adults. Apart from the dentition, all variables of the facial skeleton followed a somatic growth trajectory. Most of these variables expressed positive allometry relative to CBL, with greatest growth occurring in the vertical part of the mandible. Mastoid breadth, and gnathion to middle of occipital crest, expressed a strong secondary growth spurt at 10 y. Breadth of brain case, and basion to bend of pterygoid, followed a neural growth trajectory, scaling with negative slope relative to CBL. Sutures of the brain case (i.e., basioccipito-basisphenoid, occipito-parietal, interparietal and coronal) closed before those of the facial skeleton. Condylobasal length was found to be a 'rough indicator' of SBL and age group (adult, subadult), but not of absolute age. Suture age was not considered to be a good indicator of absolute age or age group.

Key words: Pinnipeds, skull morphology, skull growth, allometry

INTRODUCTION

Earlier cranial growth studies in pinnipeds were based on unreliable age determination techniques, including: (i) the extent of closure of cranial sutures; (ii) body length, colour of vibrissae, pelage and general appearance; (iii) ovarian structure; and (iv) baculum development (e.g., Hamilton, 1934, 1939; Lindsey, 1937, 1938; Bertram, 1940; Doutt, 1942; Rand, 1949*a*, *b*, 1950, 1956; Sivertsen, 1954; Burns & Fay, 1970). Therefore, observed growth patterns could not be quantified with any real meaning (King, 1972). It was not until the 1950s that a reasonably precise method of age determination was established, i.e., age inferred from incremental lines on or in teeth (Scheffer, 1950; Laws, 1953; McCann, 1993).

Within the Otariidae, information on cranial and mandibular growth based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), is only available for a small number of species including *Callorhinus ursinus,* northern fur seal (Scheffer & Wilke, 1953); *Zalophus californianus*, California sea lion (Orr *et al.*, 1970); and *Eumetopias jubatus,* northern (Steller) sea lion (Fiscus, 1961), and very few skull variables have been examined. Currently, there is no detailed information on cranial growth according to age (y) in southern fur seals.

In the mammalian skull, there are two growth models, neural and somatic, each with two types of growth, monophasic and biphasic (Todd & Schweiter, 1933; Scott, 1951; Moore, 1981; Sirianni & Swindler, 1985). In neural growth, skull components associated with the nervous system (i.e., braincase, orbital and otic capsules) grow rapidly during prenatal and early postnatal life, completing most of their growth well before the rest of the body (Moore, 1981). In somatic growth, all other skull components (i.e., facial skeleton) follow a more protracted growth course (Moore, 1981). After the initial growth spurt experienced during early development, growth may be reasonably constant (monophasic growth), or there may be a secondary growth spurt in older animals (biphasic growth).

Here we examine the skulls of 83 male Cape fur seals, *Arctocephalus pusillus pusillus*, from southern Africa. Specific objectives were to: (i) describe the general morphology of the skull; (ii) quantify growth of skull measurements (n = 32 variables) relative to standard body length (n = 74 animals), condylobasal length (n = 83 animals) and chronological age (n = 63 animals); and (ii) determine if condylobasal length and suture closure are useful indicators of age and/or standard body length. This study is the second in a series of papers initiated to develop baseline descriptions of Cape fur seal morphology and to examine growth patterns.

MATERIALS AND METHODS

Collection of specimens

Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34˚ 03'S, 23˚ 24'E) and East London (33˚ 03'S, 27˚ 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). From this collection[1], skulls from 59 males were selected for examination (Appendix 4.1). Apart from specimens collected before May 1992 (n = 16), all specimens were collected by the first author. One animal (PEM2238) was collected NE of the study area, at Durban.

The sample was supplemented with measurements from 24 skulls from Marine and Coastal Management (MCM), Cape Town. These skulls were from males that had been tagged as pups, and were therefore of known-age (1–12 y). MCM seal specimens are accessioned as AP followed by a number.

East coast and west coast animals

Additional skulls from Sinclair Island (West coast of southern Africa, 27˚ 40'S, 15˚ 31'E) were measured (condylobasal length only) to determine if Eastern Cape seals (n = 28 males) were of similar size to those inhabiting west coast waters (n = 12 males). PEM animals were adults 7–12$^+$ y. West coast animals were adults of unknown-age. West coast animals were collected by Dr R. W. Rand in the 1940s and housed in the South African Museum, Cape Town.

Preparation and measurement of skulls

Skulls were defleshed and macerated in water for 2–3 mo. Water was changed regularly. Skulls were then gently washed in mild detergent (or brushed with water), and air dried at room temperature. A small number of skulls were defleshed and gently boiled. Dry specimens were measured (n = 32 linear measurements) to the nearest 0.5 mm using a vernier calliper (Table 4.1, Fig. 4.1).

Variables used correspond to those reported in earlier otariid studies (Sivertsen, 1954; Orr *et al.*,1970; Repenning *et al.*, 1971; Kerley & Robinson, 1987). Variables were grouped by region in an attempt to reflect a functional cranial analysis and to assess overall skull size (Hartwig, 1993, modified) (Table 4.1).

All PEM measurements (and measurements taken form Sinclair Island skulls) were recorded by the first author. The majority of MCM measurements were recorded by the third author.

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[1] Skull measurements recorded by the first author, from 103 of these animals, were previously made avialable to S. Brunner for her honours project and subsequently published in a comparative growth study, i.e., Brunner (1998).

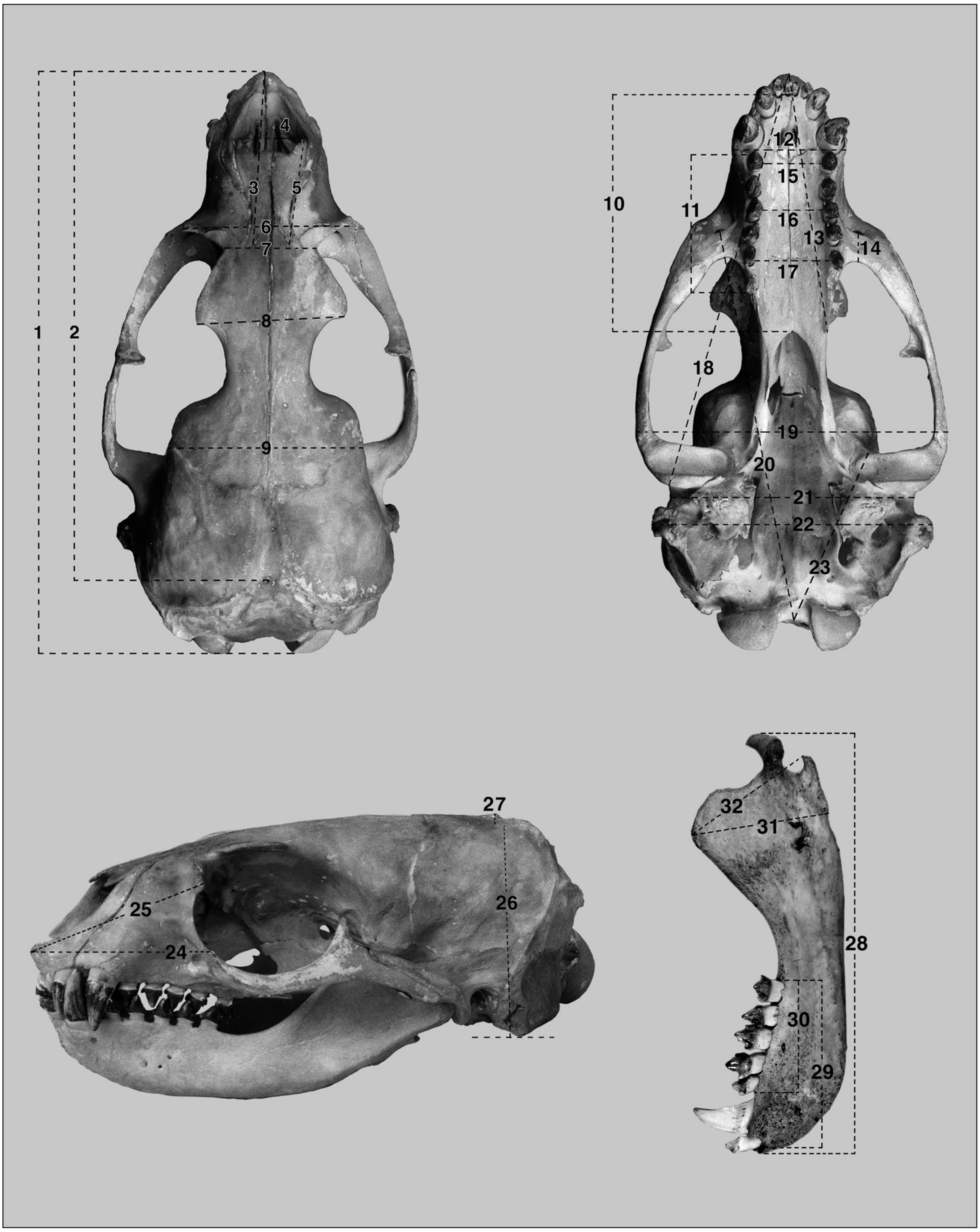

Fig. 4.1 Diagram of a Cape fur seal skull (PEM554) indicating individual measurements taken. Measurements defined in Table 4.1

Suture index

Eleven cranial sutures from 48 skulls were examined and assigned a value of 1–4, according to the degree of closure (1 = suture fully open; 2 = suture less than half-closed; 3 = suture more than half-closed; and 4 = suture completely closed) (Fig. 4.2). These values were added to give a total suture index (SI), ranging from 11 (all sutures open) to 44 (all sutures closed).

Table 4.1 ***Linear skull measurements (n = 32) taken from male Cape fur seals in this study.*** **Measurements illustrated in Fig. 4.1**

Code	Variable	Region	Function
Dorsal			
D1	Condylobasal length (posterior point on the occipital condyles to the most anterior point on the premaxilla)	–	–
D2	Gnathion to middle of occipital crest	–	R/V
D3	Gnathion to posterior end of nasals	splanchnocranium	R/V
D4	Greatest width of anterior nares (distance between the anterior margins of the nares)	nasal	R/V
D5	Greatest length of nasals (distance between the anterior and posterior margins of nasals)	nasal	R/V
D6	Breadth at preorbital processes	–	–
D7	Least interorbital constriction	frontal	–
D8	Greatest breadth at supraorbital processes	frontal	F
D9	Breadth of brain case (at the coronal suture, anterior to the zygomatic arches)	neurocranium	BC
Palatal			
P10	Palatal notch to incisors (posterior margin of first incisor alveolus to palatal notch, excluding cleft)	palate	R/V, F
P11	Length of upper postcanine row (anterior margin of postcanine one alveolus to the most posterior margin of postcanine six alveolus)	palate (dentition)	F
P12	Greatest bicanine breadth	palate	R/V, F
P13	Gnathion to posterior end of maxilla (palatal)	palate	R/V, F
P14	Breadth of zygomatic root of maxilla	zygomatic arch	F
P15	Breadth of palate at postcanine 1 (excluding the alveoli)	palate	F
P16	Breadth of palate at postcanine 3 (excluding the alveoli)	palate	F
P17	Breadth of palate at postcanine 5 (excluding the alveoli)	palate	F
P18	Gnathion to posterior border of postglenoid process	–	R/V, F
P19	Bizygomatic breadth (maximum distance between the lateral surfaces of the zygomatic arches)	zygomatic arch	F
P20	Basion to zygomatic root (anterior)	–	–
P21	Calvarial breadth (greatest transverse width across of the skull base, anterior to the mastoid)	basicranium	A
P22	Mastoid breadth (width across the processes)	basicranium	A, F
P23	Basion to bend of pterygoid (anterior of basion to anterior of pterygoid)	basicranium	BC, A, F
Lateral			
L24	Gnathion to anterior of foramen infraorbital (= lateral face length)	splanchnocranium	R/V
L25	Gnathion to posterior border of preorbital process	splanchnocranium	R/V
L26	Height of skull at base of mastoid (excluding crest)	–	
L27	Height of sagittal crest	neurocranium	BC, F
Mandibular			
M28	Length of mandible (posterior margin of condyle to anterior margin of the first incisor alveolus)	mandible	F
M29	Length of mandibular tooth row (anterior margin of the first incisor alveolus to the most posterior margin of postcanine five alveolus)	mandible (dentition)	F
M30	Length of lower postcanine row (anterior margin of postcanine one alveolus to the most posterior margin of postcanine five alveolus)	mandible (dentition)	F
M31	Height of mandible at meatus (dorsal margin of coronoid process to the base of the angularis)	mandible	A, F
M32	Angularis to coronoideus (dorsal margin of coronoid process to the top of the angularis)	mandible	F

Function: A, auditory; BC, braincase; F, feeding; R/V, respiration /vocalisation.
(measurements taken from other otariid studies - Sivertsen, 1954; Orr *et al.*, 1970; Repenning *et al.*, 1971; Kerley & Robinson, 1987; Hartwig, 1993).

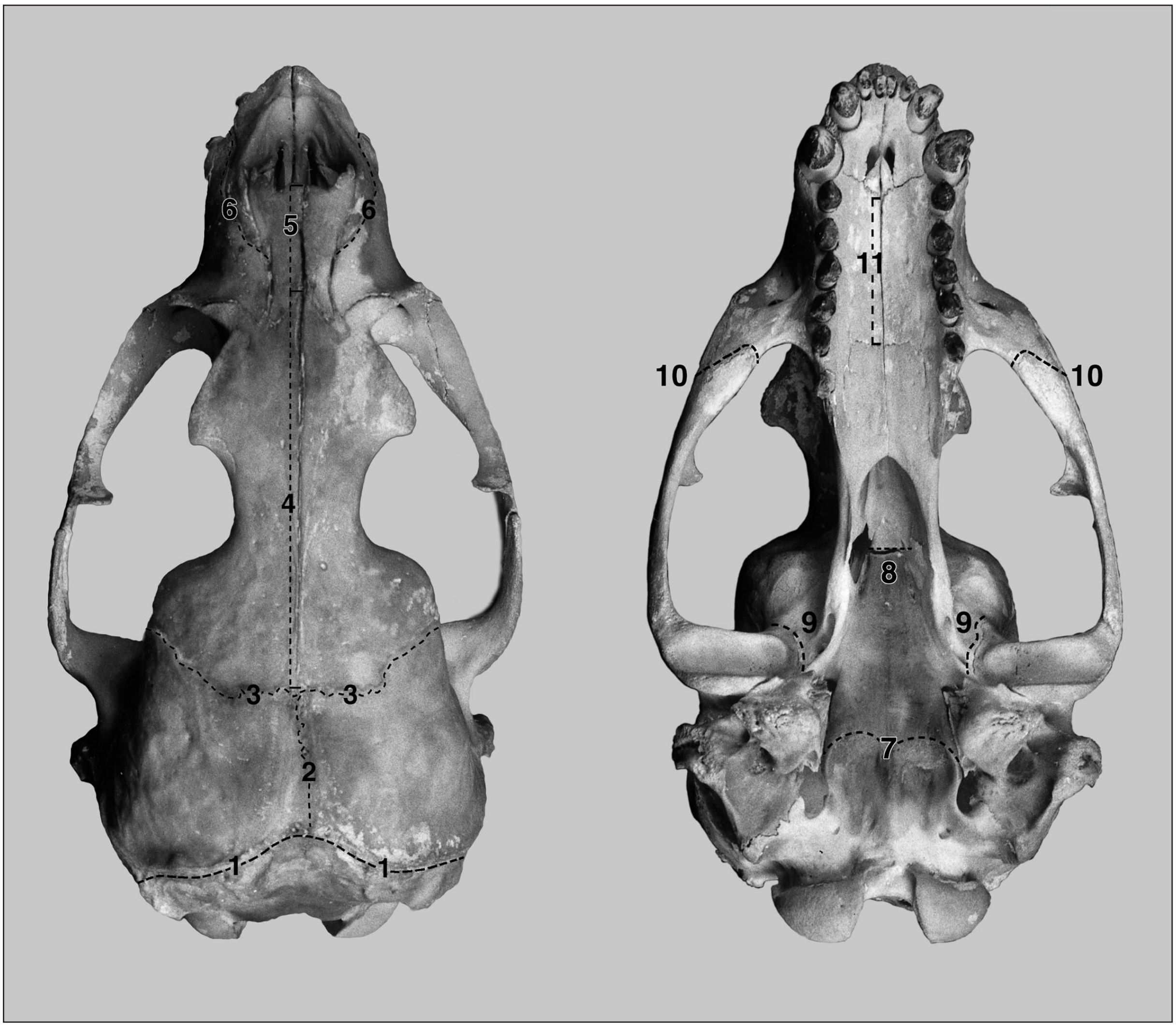

Fig. 4.2 Diagram of a Cape fur seal skull (PEM554) showing the position of sutures examined in this study.
1. occipito-parietal; 2. interparietal; 3. coronal; 4. interfrontal; 5. internasal; 6. premaxillary-maxillary; 7. basioccipito-basisphenoid; 8. basisphenoid-presphenoid; 9. squamosal-parietal; 10. squamosal-jugal; 11. maxillary.

Age determination

The total number of aged animals (known-age animals and canine aged animals) was 63. All MCM skulls (n = 24) were of known-age. Of the 59 PEM animals in the study: (i) 28 were aged from counts of incremental lines observed in the dentine of upper canines as described in Stewardson *et al*., (200X*a*), i.e., range 1–10 y; (ii) 11 were identified as adults > 12 y[2] (i.e., pulp cavity of the upper canine closed); and (iii) 20 y were not aged.

For this study, the following age groups were used: yearling (10 mo to 1 y 6 mo); subadult (1 y 7 mo to 7 y 6 mo); and adult (≥ 7 y 7 mo) (Table 4.2). Very old animals of known-age were not available for examination (estimated longevity is *c*. 20 y).

Currently, examination of tooth structure is the most precise method of age determination in pinnipeds; however, counts are not without error. For information of the reliability of this method see Oosthuizen (1997).

Classification of growth patterns

In the present study, neural and somatic growth patterns were distinguished as follows: [(mean skull measurement for adults ≥ 12 y − mean skull measurement for subadults at 7 y) × 100%]/mean skull measurement for subadults at 7 y. Where the percent increase in variable size was < 6%, growth was classified as neural, i.e., most growth was completed as subadults. Where percent increase was ≥ 6%, growth was classified as somatic, i.e., growth continued to increase in adults. Percentage increase for each variable is given in Table 4.3.

Statistical analyses

Skull measurement error

For most PEM skulls, duplicate measurements were taken of 7 randomly selected variables to assess measurement error. The 1-sample sign test was used to test the null hypothesis that the true median was equal to the hypothesised median. The Wilcoxon

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[2] In Cape fur seals, animals > 13 y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes which terminates tooth growth, hence the age group '≥ 12 y'.

sign-rank test requires the assumption that the parent population is symmetric (Gibbons & Chakraborti, 1992, p. 155). However, the distribution of data was not symmetric for all variables, thus the less powerful sign test was used. Interobserver error was not assessed.

Condylobasal length expressed in relation to standard body length

Growth in condylobasal length (CBL), relative to standard body length (SBL), was calculated as follows, using paired samples only:

$$\text{CBL (mm)}/\text{SBL (mm)} \times 100\%$$

As the approximate variance of the ratio estimate is difficult to calculate, percentages must be interpreted with caution (Cochran, 1977, p. 153).

Condylobasal length as an indicator of SBL and age

The degree of linear relationship between log CBL, log SBL and age (y) was calculated using the Spearman rank-order correlation coefficient. Linear discriminant function analysis (Mahalanobis squared distance) was used to predict the likelihood that an individual seal will belong to a particular age group (subadult, adult) using one independent variable, skull length (see Stewardson *et al.*, 200X*a* for further details). Yearlings were not examined because of small sample size, i.e., $n = 2$ yearlings.

Suture index as an indicator of age

The degree of linear relationship between suture age and canine age (y) was calculated using the Spearman rank-order correlation coefficient. Linear discriminant function analysis was used to differentiate between subadult and adult skulls using one independent variable, suture age.

Bivariate allometric regression

The relationship between value of skull measurement and: (i) SBL, (ii) CBL, (iii) age (y), was investigated using the logarithmic (base e) transformation of the allometric equation, $y = ax^b$ which may equivalently be written as $\log y = \log a + b \log x$. 'Robust' regression (Huber M-Regression) was used to fit straight lines to the transformed data. The degree of linear relationship between the transformed variables was calculated using the Spearman rank-order correlation coefficient, *r* (Gibbons & Chakraborti, 1992). Testing of model assumptions, and hypotheses about the slope of the line, followed methods described by Stewardson *et al.*, (200X*a*).

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23); Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

RESULTS

Skull measurement error

Of the 7 variables that were measured twice, measurements were reproducible at the 5% significance level (range for *p*-values: 1.0–0.08). Height of sagittal crest (L27), and height of skull at base of mastoid (L26), were difficult to measure accurately, thus must be interpreted with caution.

Skull morphology

The youngest animals in the sample were 10 mo of age (Fig. 4.3a; Table 4.3). In these individuals, the skull was *c.* 160 mm in length (D1) and 87 mm wide (P19). The brain case was relatively large, measuring 120 mm (75% of CBL) from the most posterior end of nasals to the most posteriorly projecting point on the occipital bone, in the mid-sagittal plane. There were no signs of bony ridges or prominences. Relative to CBL, the face and mandible were short. Milk dentition had not been completely replaced by permanent teeth in animal AP4999. It was clear that the deciduous canines persist in some animals until their tenth month.

In adults 10 y of age, the skull was rugose, with heavy bony deposits (Fig. 4.3b; Table 4.3). Mean length (D1) and breadth (P19) was 248 mm and 142 mm, respectively. The braincase was 157 mm in length (63% of CBL), and a sagittal crest was present (4.4–12.0 mm in height, $n = 5$). The forehead was convex at the supraorbital region. Relative to CBL, the face was long, with long nasals that flared anteriorly. The ratio of nasal breadth to length was 1 : 1.5. The palate was long, moderately broad and arched. The ratio of palatal breadth (P15–17) to palatal length (P10) was 1 : 3–4. The maxillary shelf at the root of the zygomatic process (P14) was very short in an anterio-posterior direction (16 mm; 6% of CBL). The mandible was long with a broad coronoid process. The tooth rows were parallel, with enlarged third incisor; large canines; robust, tricuspid postcanines (PC); and a slight diastema between upper PC 5 and 6 (Repenning *et al.*, 1971; present study). Dental formula was (I $^3/_2$ C $^1/_1$ PC $^6/_5$).

East coast and west coast animals

Available data suggested that skulls from adult males, 7–12$^+$ y, from Eastern Cape fur seals (mean 246.6 ± 2.5 mm; range 213.7–266.8 mm; $n = 28$) were significantly smaller than skulls from adult animals inhabiting west coast waters (mean 259.4 ± 4.5 mm; range 225.6–282.1 mm; $n = 12$) (at the 5% significance level two sample t-test^2: $t = -2.48$; $P = 0.024$; $df = 17$).

However, skulls from adult males, > 12 y, from the Eastern Cape (mean 255.7 ± 2.6 mm; range 239.9–266.6 mm; $n = 11$) were not significantly smaller than skulls from adult animals inhabiting west coast waters (mean 259.4 ± 4.5 mm; range 225.6–282.1 mm; $n = 12$) (at the 5% significance level two sample t-test^2: $t = -0.71$; $P = 0.49$; $df = 17$).

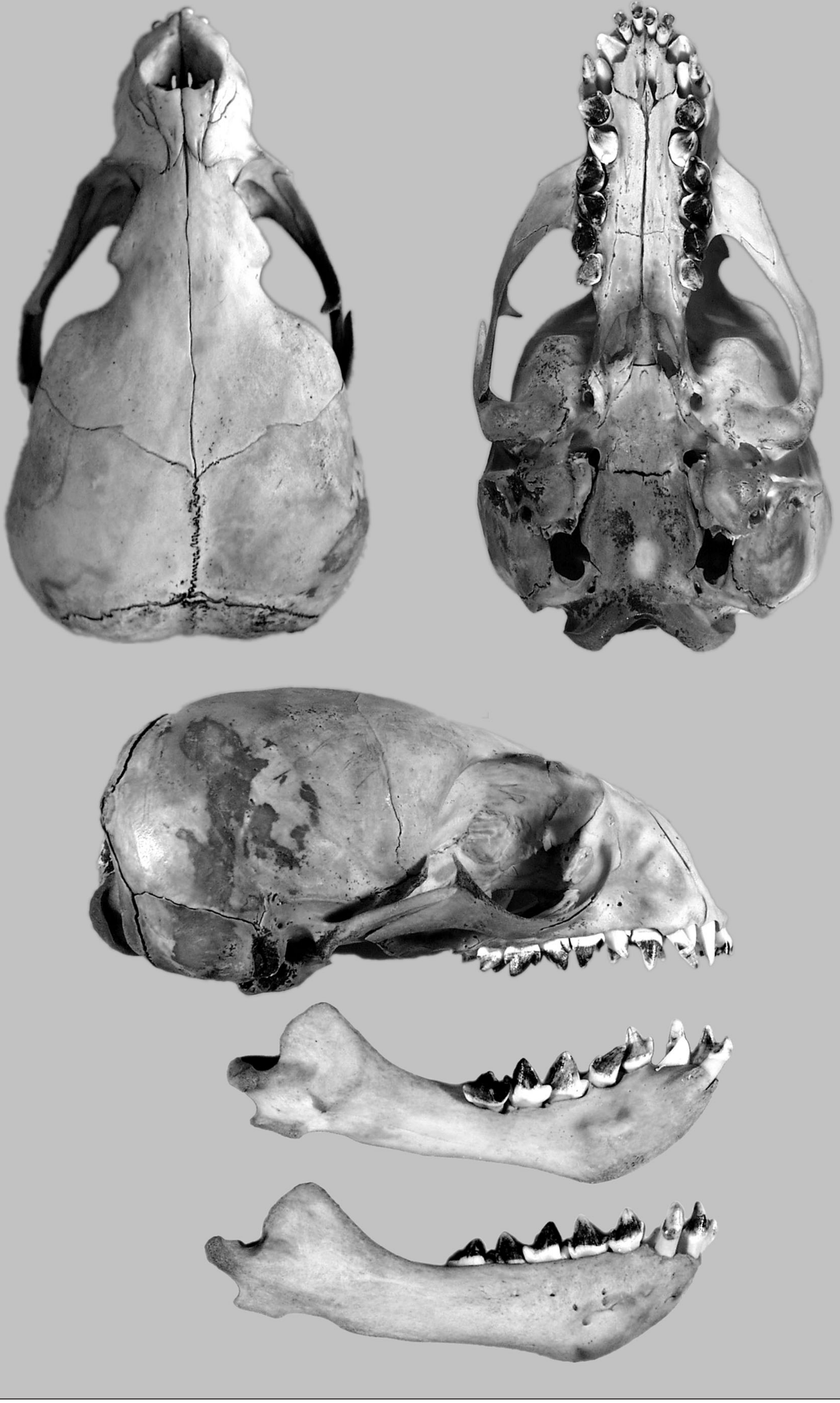

Fig. 4.3a Size and shape of the Cape fur seal skull: juvenile 10 mo (AP4999).

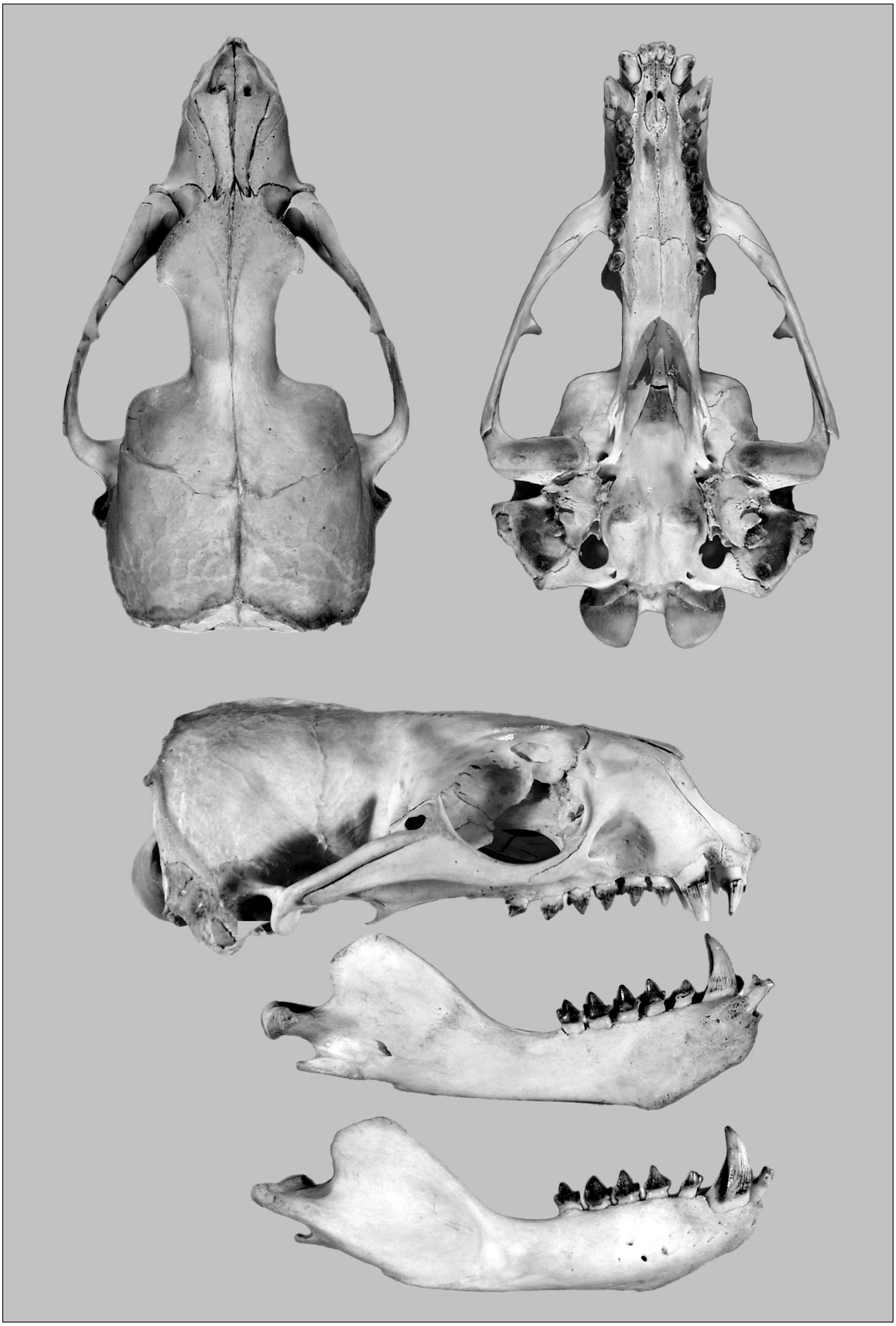

Fig. 4.3b Size and shape of the Cape fur seal skull: adult 10 y (AP4992).

Table 4.2 *The age distribution of Cape fur seals*

Age group	Age[a] (y)	Frequency	Percentage
Yearling	1	2	3.2
Subadult	2	2	3.2
	3	2	3.2
	4	8	12.7
	5	4	6.3
	6	4	6.3
	7	12	19.0
Adult	8	7	11.1
	9	5	7.9
	10	5	7.9
	≥ 12	12	19.0
Total		**63**	**100**

[a] **Animals 1–10 y**: 23 MCM animals were of known-age; 28 PEM animals were aged from counts of incremental lines observed in the dentine of upper canine.
Animals ≥ 12 y: one MCM animals was 12 y; 11 PEM males were > 12 y, i.e., the pulp cavity of the upper canine was closed.

Condylobasal length expressed in relation to SBL

Relative to SBL, condylobasal length decreased with increasing SBL, i.e., 19.4% (yearlings), 15.5% (subadults), 13.8% (adults, 8–10 y) and 13.6% (adults ≥ 12 y) (Table 4.4).

Condylobasal length as an indicator of age

Condylobasal length continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). In animals 1–10 y, growth in skull length was highly positively correlated with age (y) ($r = 0.89$, $n = 51$) (Fig. 4.4b). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate (the residuals were not scattered randomly about zero, see Weisberg, 1985, p. 23). Thus, CBL could not be used as a reliable indicator of absolute age. The coefficient of variation in skull length for young males 1–5 y (12.3%) was considerably higher than in older males (8–10 y, 4.3%; ≥ 12 y, 5.7%) (Table 4.3).

Although CBL was not a useful indicator of absolute age, it was a ‘rough indicator’ of age group. When skull length is known, the following linear discriminant functions can be used to categorise each observation into one of two age groups–adult or subadult:

$$y_1 = -98.43 + 0.91x$$
$$y_2 = -129.06 + 1.05x$$

where x = skull length (mm); subscript 1 = subadult; and subscript 2 = adult. The seal is classified into the age group associated with the linear discriminant function which results in the minimum value. Of the 61 observations in this study 85% were correctly classified using this method (Table 4.5).

Condylobasal length as an indicator of SBL

Skull length was highly, positively correlated with SBL ($r = 0.93$, $n = 74$; Fig. 4.4a). When CBL is known, the following equation (linear least squares fit; untransformed data) can be used as a ‘rough indicator’ of SBL:

$$y = -4.11 + 1.69x$$

which may equivalently be written as SBL = $e^{-4.11} \times \text{CBL}^{1.69}$, where the S.E. of the intercept is 0.28 and the S.E. of the slope is 0.05 ($n = 74$).

Suture index as an indicator of age

The sequence of suture closure according to age (y) and age group is depicted in Table 4.6. Sutures *i–xi* showed signs of partial closure at different times, and the time taken to reach full closure was different for each suture. The cranial sutures (basioccipito-basisphenoid, coronal, occipito-parietal and interparietal) were the first to partially close. The squamosal-jugal, squamosal-parietal, maxillary, premaxillary-maxillary, and interfrontal were the last to show signs of partial closure (order of partial closure unknown), with the basisphenoid-presphenoid and internasal remaining fully open in all specimens examined.

The exact sequence of full closure for all 11 sutures could not be established because animals of known-age, > 12 y, were not available for analysis. However, the basioccipito-basisphenoid and occipito-parietal were the first sutures to fully close in animals 3 and 4 y, respectively; followed by the interparietal in some animals ≥ 7 y; and then the coronal or squamosal-jugal in animals ≥ 12 y.

In animals 1–10 y, suture age was highly positively correlated with age ($r = 0.81$, $p = 0.000$, $n = 38$) (Fig. 4.5c). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate.

Furthermore, linear discriminant function could not be used satisfactorily to categorise each observation into age groups, i.e., of the 46 animals examined, all subadults ($n = 26$) were correctly classified; however, seven (35%) of the 20 adults were incorrectly classified as subadults.

Suture age was highly positively correlated with SBL ($r = 0.89$, $p = 0.000$, $n = 63$) (Fig. 4.5a). Information on suture age as an indicator of physiological maturity is presented elsewhere (Stewardson *et al.*, 200Y).

Bivariate allometric regression

Regression statistics for skull measurements (D1–M32) on SBL, CBL and age (y) are given in Appendix 4.2–4.4. Overall, correlation coefficients

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[2] The two sample t-test used in the above analysis does not use the assuption of equal variance and D.F. ≠ n – 1.

Table 4.3 ***Summary statistics for dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull variables according to age (y) and age group.*** **Data presented as mean skull variable in mm ± S.E., followed by coefficient of variation in round brackets, and skull variable expressed as a percentage of skull length. Maximum value of each variable (males of unknown-age), and classification of growth pattern, are also presented.**

Age group	**Age (y)**	***n*[a]**	**D1**	**D2**	**D3**	**D4**	**D5**	**D6**	**D7**
Yearling	1	2	159.7 ± 2.6 (2.3)	144.8 ± 2.4 (2.3) 90.7%	54.1 ± 1.0 (2.6) 33.9%	20.3 ± 0.1 (0.7) 12.7%	25.1 ± 1.6 (8.8) 15.7%	40.8 ± 0.1 (0.3) 25.6%	21.6 ± 0.3 (1.6) 13.5%
Subadult	2	2	174.5 ± 7.2 (5.8)	148.7 ± 2.1 (2.0) 85.2%	56.3 ± 2.6 (6.4) 32.2%	17.9 ± 0.4 (3.2) 10.3%	25.7 ± 0.7 (3.9) 14.7%	45.0 ± 3.8 (11.8) 25.8%	22.1 ± 1.3 (8.0) 12.6%
	3	2	196.2 ± 1.8 (1.3)	162.8 ± 1.9 (1.7) 83.0%	64.9 ± 1.9 (4.1) 33.1%	21.5 ± 1.0 (6.6) 11.0%	33.1 ± 1.9 (8.1) 16.9%	48.6 ± 0.3 (0.7) 24.8%	24.7 ± 0.9 (5.1) 12.6%
	4	8	205.2 ± 4.7 (6.4)	173.6 ± 4.0 (6.6) 84.6%	71.1 ± 1.8 (7.1) 34.7%	22.8 ± 0.3 (4.2) 11.1%	34.1 ± 1.3 [6] (9.4) 16.8%	54.6 ± 1.3 (6.7) 26.6%	29.5 ± 0.8 (8.0) 14.4%
	5	4	217.0 ± 4.3 (4.0)	183.5 ± 3.4 (3.7) 84.6%	75.7 ± 1.8 (4.8) 34.9%	24.2 ± 0.5 (4.4) 11.1%	37.2 ± 0.8 (4.5) 17.1%	57.3 ± 2.3 (8.0) 26.4%	31.0 ± 1.1 (7.1) 14.3%
	6	4	220.6 ± 3.4 (3.1)	187.6 ± 4.4 (4.7) 85.0%	76.1 ± 0.7 [3] (1.6) 35.0%	23.6 ± 1.5 (12.9) 10.7%	39.0 ± 2.7 (13.9) 17.7%	59.9 ± 0.5 (1.6) 27.1%	31.2 ± 0.7 (4.6) 14.1%
	7	12	230.6 ± 2.1 (3.2)	197.8 ± 1.9 [11] (3.2) 85.5%	81.3 ± 1.5 (6.5) 35.3%	25.0 ± 0.6 [11] (7.8) 10.8%	40.1 ± 0.6 (5.1) 17.4%	63.6 ± 1.0 (5.6) 27.6%	33.9 ± 0.7 (6.9) 14.7%
	2–7	**32**	**215.7 ± 3.2 (8.3)**	**183.0 ± 2.9 [31] (9.0) 90.9%**	**74.8 ± 1.5 [31] (11.1) 34.7%**	**23.4 ± 0.4 [31] (10.4) 10.9%**	**37.0 ± 0.9 [30] (13.0) 17.1%**	**58.0 ± 1.2 (11.3) 26.9%**	**30.8 ± 0.7 (12.8) 14.3%**
Adult	8	7	236.8 ± 4.5 (5.0)	206.9 ± 5.6 (7.1) 87.4%	83.6 ± 2.3 (7.2) 35.3%	26.5 ± 0.9 [6] (8.7) 11.2%	41.6 ± 1.7 [6] (9.9) 17.6%	66.0 ± 1.5 (6.0) 27.9%	36.5 ± 1.2 (8.5) 15.4%
	9	5	242.2 ± 1.6 (1.5)	206.5 ± 5.3 [4] (5.1) 85.1%	84.3 ± 1.9 [4] (4.6) 34.8	28.2 ± 1.2 (9.4) 11.6%	40.5 ± 2.0 [4] (9.9) 16.7%	67.2 ± 1.5 [4] (4.3) 27.7%	38.4 ± 1.9 [4] (9.9) 15.8%
	10	5	248.2 ± 4.7 (4.2)	220.1 ± 6.1 (6.1) 88.7%	89.9 ± 2.5 (6.3) 36.2%	29.0 ± 1.0 (8.1) 11.7%	44.3 ± 2.1 (10.7) 17.9%	68.7 ± 3.2 (10.3) 27.7%	38.6 ± 0.7 [4] (3.6) 15.3%
	8–10	**17**	**241.7 ± 2.5 (4.3)**	**210.9 ± 3.5 [16] (6.7) 87.2%**	**85.7 ± 1.4 [16] (6.9) 35.5%**	**27.8 ± 0.6 [16] (9.1) 11.5**	**42.2 ± 1.1 [15] (10.2) 17.5%**	**67.2 ± 1.2 [16] (7.1) 27.8%**	**37.6 ± 0.8 [15] (7.8) 15.5%**
	≥ 12	12	249.9 ± 4.1 (5.7)	225.3 ± 5.0 [11] (7.3) 90.1%	92.4 ± 2.2 (8.1) 37.0%	29.6 ± 0.8 (9.0) 11.9%	47.0 ± 1.4 (10.1) 18.8%	69.1 ± 1.8 [10] (8.4) 27.9%	38.0 ± 1.2 [10] (9.6) 15.2%
Total		**63**	**63**	**60**	**61**	**61**	**59**	**60**	**59**
Mean for males ≥ 200 cm [max. value in brackets][b]			259.2 ± 7.0 [275.4]	234.8 ± 9.4 [254.4]	97.4 ± 4.7 [108.9]	30.6 ± 1.1 [33.8]	50.2 ± 2.9 [57.6]	72.3 ± 4.0 [3] [77.0]	38.4 ± 0.5 [42.8]
Growth pattern, Evidence of a SGS[c]			Somatic, 8% No	Somatic, 14% 10 y (strong)	Somatic, 14% 10 y (weak)	Somatic, 18% No	Somatic, 17% (see text)	Somatic, 9% No	Somatic, 12% No

Variables: D1 condylobasal length; **D2** gnathion to middle of occipital crest; **D3** gnathion to posterior end of nasals; **D4** greatest width of anterior nares; **D5** greatest length of nasals; **D6** breadth at preorbital processes; **D7** least interorbital constriction.

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were moderately to strongly positive, i.e., most points on the scatter plot approximate a straight line with positive slope, $r \geq 0.70$. Exceptions included breadth of brain case on SBL, CBL and age (y) ($r = 0.3–0.4$); length of upper PC row on age (y) ($r = 0.59$), and breadth of zygomatic root of maxilla on age (y) ($r = 0.57$). SBL was strongly positively correlated with age (y) ($r = 0.87$). Although correlation coefficients indicate that linearity was reasonably well approximated for most variables by log-log transformations, a linear relation did not necessarily best describe the relationship.

Growth of skull variables according to region

Most variables within a given region were significantly positively correlated with each other, $r \geq 0.70$ (Appendix 4.5). Exceptions were: (i) breadth of palate at PC 5 (P17) with length of upper PC row (P11) ($r < 0.7$; significant at 0.01); and (ii) breadth of brain case (D9) with height of sagittal crest (L27) ($r = 0.25$; not significant).

Neurocranium region (D9, L27)

Breadth of brain case (D9) followed a neural growth pattern, with most growth completed by 6 y (84 mm) (Fig. 4.6). Overall growth scaled with negative slope (b = 0.17) relative to CBL. In yearlings, the brain case was proportionally long, i.e., 75% of CBL in yearlings, and 63% of CBL at 10 y. Growth in length of the brain case (31% at 10 y relative to yearlings, RTY) was much greater than growth in breadth (8% at 10 y, RTY). The ratio of breadth to length increased from 1: 1.5 (yearlings) to 1 : 1.9 y (10 y).

Height of sagittal crest (L27) appeared to follow a somatic growth pattern; however, there was great variation among individuals of similar age. The crest

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Age group	Age (y)	*n*[a]	D8	D9	P10	P11	P12	P13	P14
Yearling	1	2	38.2 ± 0.4 (1.5) 23.9%	78.0 ± 0.4 (0.6) 48.8%	64.3 ± 0.7 (1.4) 40.2%	40.5 [1*] (–) 25.0%	33.8 ± 1.2 (4.8) 21.1%	73.0 ± 0.5 (1.0) 45.7%	12.9 ± 0.5 (5.5) 8.1%
Subadult	2	2	37.8 ± 1.9 (7.1) 21.7%	78.7 ± 1.3 (2.2) 45.1%	66.2 ± 3.0 (6.4) 37.9%	43.2 ± 0.3 (0.8) 24.7%	32.5 ± 1.6 (6.8) 18.6%	77.7 ± 1.2 (2.1) 44.5%	11.3 ± 0.3 (3.8) 6.5%
	3	2	39.5 [1*] (–) 20.3%	81.7 ± 4.0 (6.8) 41.6%	82.3 ± 2.8 (4.8) 42.0%	62.1 ± 0.7 (1.5) 31.6%	35.2 ± 0.8 (3.0) 17.9%	89.3 ± 0.1 (0.2) 45.5%	12.4 ± 0.3 (3.4) 6.3%
	4	8	45.6 ± 1.6 (10.2) 22.2%	81.7 ± 1.1 (3.7) 39.8%	87.9 ± 2.5 (8.1) 42.8%	49.8 ± 0.4 (2.5) 24.3%	39.6 ± 0.8 (5.5) 19.3%	94.2 ± 2.7 (8.1) 45.9%	12.7 ± 0.3 (7.0) 6.2%
	5	4	46.7 ± 2.0 (8.4) 21.5%	82.2 ± 1.6 (3.9) 37.9%	88.6 ± 2.3 [3] (4.4) 41.6%	54.2 ± 2.4 (9.0) 25.0%	42.5 ± 1.3 (6.1) 19.6%	101.9 ± 3.2 (6.2) 47.0%	14.5 ± 0.7 (9.5) 6.7%
	6	4	46.3 ± 1.3 (5.6) 21.0%	83.7 ± 1.7 (4.0) 37.9%	94.1 ± 1.1 (2.7) 42.3%	54.9 ± 0.8 (3.3) 24.7%	43.0 ± 0.7 (3.4) 19.6%	103.9 ± 1.4 (3.0) 47.0%	14.1 ± 0.6 (8.8) 6.4%
	7	12	52.5 ± 1.2 [11] (7.7) 22.7%	84.1 ± 0.8 (3.3) 36.4%	97.8 ± 1.7 (6.0) 42.4%	57.2 ± 0.8 (4.8) 24.8%	45.9 ± 0.5 [11] (3.3) 19.8%	110.6 ± 1.3 (4.0) 48.0%	13.8 ± 0.4 (10.4) 6.0%
	2–7	**32**	**47.6 ± 1.0 [30] (12.0) 22.1%**	**82.7 ± 0.6 (3.9) 38.3%**	**90.9 ± 1.7 [31] (10.6) 42.2%**	**54.2 ± 0.9 (9.3) 25.1%**	**41.9 ± 0.8 [31] (10.3) 19.5%**	**101.3 ± 1.9 (10.6) 46.9**	**13.4 ± 0.3 (10.6) 6.2%**
Adult	8	7	53.6 ± 0.4 [5] (1.8) 22.8%	84.6 ± 2.0 (6.3) 35.7%	99.6 ± 2.5 (6.6) 42.1%	57.7 ± 1.8 (8.4) 24.4%	47.9 ± 1.3 (7.2) 20.2%	112.0 ± 2.6 (6.0) 47.3%	14.4 ± 0.5 (9.7) 6.1%
	9	5	56.5 ± 2.8 [3] (8.6) 23.2%	83.1 ± 1.3 (3.0) 34.3%	105.6 ± 0.7 (1.5) 43.6%	60.2 ± 1.2 (4.4) 24.9%	46.6 ± 0.8 (3.7) 19.2%	115.0 ± 0.9 [4] (1.5) 47.3%	14.4 ± 0.7 (11.0) 5.9%
	10	5	57.3 ± 1.9 (7.5) 23.1%	84.2 ± 0.9 (2.3) 33.9%	109.3 ± 3.7 (7.6) 44.0%	59.3 ± 1.2 (4.7) 23.9%	51.1 ± 2.8 (12.2) 20.6%	117.2 ± 1.9 (3.6) 47.2%	16.0 ± 1.1 (14.9) 6.4%
	8–10	**17**	**55.7 ± 1.0 [13] (6.6) 23.0%**	**84.0 ± 0.9 (4.5) 34.8%**	**104.2 ± 1.8 (6.9) 43.1%**	**58.9 ± 0.9 (6.3) 24.4%**	**48.4 ± 1.0 (8.9) 20.0%**	**114.4 ± 1.3 [16] (4.7) 47.3%**	**14.8 ± 0.4 (12.3) 6.1%**
	≥ 12	12	58.0 ± 2.1 (12.4) 23.2%	84.0 ± 1.3 (5.2) 33.6%	106.3 ± 2.0 (6.3) 42.0%	62.0 ± 1.6 (8.6) 24.5%	54.1 ± 1.1 (6.8) 21.4%	118.4 ± 2.4 (6.8) 46.7%	17.2 ± 0.4 (7.7) 6.8%
Total		**63**	**57**	**63**	**62**	**62**	**62**	**62**	**63**
Mean for males ≥ 200 cm [max. value in brackets][b]			62.8 ± 2.3 [69.1]	85.2 ± 0.9 [3] [90.0]	112.8 ± 4.4 [123.0]	60.5 ± 2.1 [70.5]	53.7 ± 3.3 [62.2]	123.7 ± 4.1 [134.6]	17.4 ± 1.0 [20.0]
Growth pattern, Evidence of a SGS[c]			Somatic, 10% 7 y (weak)	Neural, 0% No	Somatic, 9% No	Somatic, 8% No	Somatic, 18% (see text)	Somatic, 7% No	Somatic, 25% No

Variables: D8 greatest breadth at supraorbital processes; **D9** breadth of brain case; **P10** palatal notch to incisors; **P11** length of upper postcanine row; **P12** greatest bicanine breadth; **P13** gnathion to posterior end of maxilla; **P14** breadth of zygomatic root of maxilla.

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was absent in juveniles and young subadults. Evidence of crest formation was apparent in one 4 y old (*n* = 7), two 6 y olds (*n* = 4), eight 7 y olds (*n* = 8), and all males ≥ 8 y. Maximum crest height was 11–12 mm (*n* = 4). There was some evidence of a very slight secondary growth spurt in some males at *c.* 10 y, but sample size was too small to confirm this observation.

Basicranium region (P21, P22, P23)

Calvarial breadth (P21) followed a somatic, monophasic growth pattern. Overall growth in variable size increased in proportion (*b* = 1) to skull size, increasing by 49% at 10 y (RTY).

Mastoid breadth (P22) followed a somatic growth pattern. Overall growth scaled with positive slope (*b* = 1.29) relative to CBL, increasing by 80% at 10 y (RTY). A prominent secondary growth spurt was apparent at 10 y (Fig. 4.7).

Basion to bend of pterygoid (P23) followed a neural growth pattern, with most growth competed by 7 y (76 mm). Overall growth in variable size was negatively allometric relative to CBL.

Frontal region (D7, D8)

Least interorbital constriction (D7) followed a somatic, monophasic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 79% at 10 y (RTY). Most growth was completed by 9 y.

Greatest breadth at supraorbital processes (D8) followed a somatic growth pattern. Overall growth scaled with a very slight positive slope (*b* = 1.03) relative to CBL, increasing by 50% at 10 y (RTY). A weak secondary growth spurt was apparent at 7 y.

Zygomatic arch (P14, P19)

Breadth of zygomatic root at maxilla (P14) followed a somatic, monophasic growth pattern. Overall growth was isometric relative to CBL, increasing by 24% at 10 y (RTY).

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Age group	Age (y)	n[a]	P15	P16	P17	P18	P19	P20	P21
Yearling	1	2	14.1 ± 0.7 (6.5) 8.8%	18.4 ± 0.5 (3.8) 11.5%	20.8 ± 0.1 (0.3) 13.0%	111.1 ± 0.3 (0.3) 69.6%	86.6 ± 0.5 (0.8) 54.2%	109.3 ± 2.2 (2.8) 68.5%	77.3 ± 2.0 (3.7) 48.4%
Subadult	2	2	13.0 ± 0.4 (3.8) 7.4%	16.7 ± 0.3 (2.5) 9.6%	20.7 ± 0.7 (4.8) 11.9%	122.4 ± 3.4 (3.9) 70.2%	92.6 ± 3.0 (4.5) 53.1%	120.0 ± 5.7 (6.7) 68.9%	77.8 ± 1.5 (2.6) 44.6%
	3	2	16.3 ± 0.2 (1.7) 8.3%	19.6 [1*] (–) 10.1%	25.0 ± 1.6 (8.8) 12.7%	141.0 ± 1.3 (1.3) 71.9%	103.8 ± 1.7 (2.2) 52.9%	133.0 ± 0.4 (0.4) 67.8%	87.3 ± 0.7 (1.0) 44.5%
	4	8	17.2 ± 0.5 (7.7) 8.4%	21.9 ± 0.6 (7.2) 10.6%	26.0 ± 1.1 (12.3) 12.7%	150.0 ± 4.1 (7.8) 73.1%	111.0 ± 2.7 (6.8) 54.1%	139.8 ± 3.2 (6.5) 68.1%	93.6 ± 2.4 (7.4) 45.6%
	5	4	20.7 ± 1.2 [3] (9.8) 9.4%	23.8 ± 1.1 [3] (7.9) 10.8%	30.1 ± 1.7 (11.2) 13.9%	162.4 ± 4.7 [3] (5.0) 74.1%	121.9 ± 3.6 (5.9) 56.2%	148.3 ± 2.6 (3.5) 68.4%	104.0 ± 2.3 (4.4) 47.9%
	6	4	19.6 ± 0.4 (4.2) 8.9%	23.4 ± 0.6 (6.1) 10.5%	29.2 ± 1.2 (9.1) 12.9%	162.1 ± 1.7 [4] (2.1) 74.2%	121.0 ± 3.2 (6.0) 54.5%	150.2 ± 1.3 (1.9) 68.0%	102.6 ± 0.4 (0.8) 46.5%
	7	12	20.7 ± 1.2 [8] (16.0) 8.9%	25.0 ± 0.4 [8] (4.5) 10.7%	30.5 ± 0.7 [11] (7.6) 13.2%	173.2 ± 1.8 [10] (3.3) 74.9%	125.7 ± 2.1 (5.7) 54.5%	157.5 ± 1.4 (3.0) 68.3%	107.5 ± 1.3 (4.3) 46.6%
	2–7	**32**	**18.6 ± 0.6 [27] (16.2) 8.7%**	**22.8 ± 0.5 [26] (11.5) 10.6%**	**28.2 ± 0.7 [31] (13.4) 13.0%**	**158.4 ± 3.0 [28] (10.3) 73.8%**	**117.6 ± 2.0 (9.8) 54.5%**	**147.2 ± 2.1 (8.2) 68.2%**	**99.9 ± 1.7 (9.8) 46.3%**
Adult	8	7	23.4 ± 0.8 [6] (8.8) 9.9%	26.3 ± 0.9 [6] (8.3) 11.1%	32.6 ± 0.9 (7.3) 13.8%	178.5 ± 4.2 (6.3) 75.4%	135.1 ± 3.3 (6.4) 57.1%	161.0 ± 3.4 [6] (5.6) 68.0%	111.8 ± 2.5 (5.4) 47.4%
	9	5	22.6 ± 0.7 [4] (6.5) 9.3%	25.0 ± 0.9 [4] (7.1) 10.3%	29.8 ± 1.1 (8.1) 12.3%	184.3 ± 2.0 [4] (2.1) 75.9%	137.1 ± 1.8 (2.9) 56.6%	164.6 ± 0.7 (1.0) 68.0%	112.0 ± 1.5 (3.0) 46.3%
	10	5	26.7 ± 1.1 [4] (8.1) 10.6%	27.0 ± 1.8 (14.8) 10.9%	35.7 ± 0.3 [4] (1.9) 14.1%	189.0 ± 3.4 (4.1) 76.2%	141.8 ± 2.9 (4.6) 57.1%	173.3 ± 2.7 [4] (3.1) 68.7%	115.5 ± 2.9 (5.7) 46.6%
	8–10	**17**	**24.1 ± 0.7 [14] (10.3) 9.9%**	**26.2 ± 0.7 [15] (10.6) 10.8%**	**32.5 ± 0.8 [16] (9.3) 13.4%**	**183.2 ± 2.4 [16] (5.2) 75.8%**	**137.7 ± 1.7 (5.2) 57.0%**	**165.2 ± 2.0 [15] (4.8) 68.2%**	**113.0 ± 1.4 (4.8) 46.8%**
	≥ 12	12	28.0 ± 0.8 [11] (11.3) 11.0%	30.0 ± 0.8 [11] (8.5) 11.8%	35.8 ± 0.6 (6.5) 14.1%	195.3 ± 2.1 [11] (3.4) 76.0%	150.6 ± 2.1 (4.7) 59.5%	173.6 ± 1.8 (3.7) 68.5%	121.0 ± 1.6 (4.3) 47.8%
Total		**63**	**54**	**54**	**61**	**57**	**63**	**61**	**63**
Mean for males ≥ 200 cm [max. value in brackets][b]			28.7 ± 2.5 [35.4]	28.9 ± 1.4 [32.7]	36.5 ± 1.6 [40.9]	197.0 ± 6.3 [211.6]	140.0 ± 2.0 [158.9]	174.8 ± 4.9 [183.4]	120.2 ± 2.7 [126.1]
Growth pattern, Evidence of a SGS[c]			Somatic, 35% No	Somatic, 20% No	Somatic, 17% (see text)	Somatic, 13% No	Somatic, 20% No	Somatic, 10% No	Somatic, 13% No

Variables: P15 breadth of palate at postcanine 1; **P16** breadth of palate at postcanine 3; **P17** breadth of palate at postcanine 5; **P18** gnathion to hind border of postglenoid process; **P19** bizygomatic breadth; **P20** basion to zygomatic root; **P21** calvarial breadth.

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Bizygomatic breadth (P19) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope (*b* = 1.12) relative to CBL, increasing by 64% at 10 y (RTY). The ratio of bizygomatic breadth to CBL was 1 : 1.8 in yearlings and adults. Bizygomatic breadth was generally the widest part of the skull; however, mastoid breadth exceeded bizygomatic breadth in 10 animals (7 subadults; 3 adults).

Splanchnocranium region (D3, L24, L25)

Gnathion to posterior end of nasals (D3) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 66% at 10 y (RTY). A weak secondary growth spurt was apparent at 10 y.

Gnathion to foramen infraorbital (L24) and gnathion to posterior border of preorbital process (L25) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope (*b* = 1.26, 1.25) relative to CBL, increasing by 62% and 70% at 10 y (RTY), respectively.

Nasal region (D4, D5)

Width of anterior nares (D4) followed a somatic, monophasic growth pattern. Overall growth was isometric relative to CBL (Fig. 4.8), increasing by 43% at 10 y (RTY).

Greatest length of nasals (D5) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 76% at 10 y (RTY). There was some evidence of a very slight secondary growth spurt at 10 y, but this may have been an effect of sampling. The ratio of nasal breadth to length increased from 1: 1.2 (yearlings) to 1 : 1.5 y (10 y).

Palatal region (P10, P11, P12, P13, P15, P16, P17)

Palatal notch to incisor (P10) and gnathion to posterior end of maxilla (P13), followed a somatic

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Age group	Age (y)	n[a]	P22	P23	L24	L25	L26**	L27**	M28
Yearling	1	2	74.8 ± 2.1 (4.0) 46.9%	59.6 ± 0.9 (2.0) 37.3%	45.7 ± 2.5 (7.6) 28.6%	48.3 ± 0.4 (1.2) 30.3%	73.1 [1*]	0.0	98.9 ± 0.1 (0.1) 62.9%
Subadult	2	2	82.0 ± 3.2 (5.4) 47.0%	62.6 ± 4.1 (9.2) 35.9%	42.2 ± 2.7 (9.0) 24.2%	52.2 ± 1.7 (4.5) 29.9%	72.3 ± 0.9	0.0 [1]	114.8 ± 9.1 (11.2) 65.8%
	3	2	93.9 ± 0.7 (1.0) 47.8%	66.5 ± 0.7 (1.4) 33.9%	57.1 ± 3.6 (8.9) 29.1%	59.1 ± 0.3 (6.7) 30.1%	– [0]	0.0	126.0 ± 1.2 (1.3) 64.2%
	4	8	100.9 ± 2.8 (7.9) 49.2%	69.8 ± 1.2 (5.0) 34.0%	61.4 ± 2.7 (12.4) 29.9%	64.3 ± 2.5 (11.2) 31.3%	77.6 ± 0.6 [4]	0.07 ± 0.07 [7]	136.5 ± 3.8 (7.9) 66.5%
	5	4	109.8 ± 3.5 (6.3) 50.6%	74.6 ± 0.9 (2.5) 34.4%	63.1 ± 1.2 (3.9) 29.1%	69.3 ± 1.8 (5.2) 31.9%	86.0 ± 2.1 [3]	0 [2]	147.2 ± 4.8 (6.5) 67.8%
	6	4	111.5 ± 1.6 (3.2) 50.3%	73.8 ± 0.4 (1.2) 33.6%	64.5 ± 1.8 (6.2) 29.8%	71.9 ± 1.4 (4.3) 32.5%	86.5 ± 0.8 [3]	0.7 ± 0.5 [4]	149.7 ± 1.9 (2.9) 68.0%
	7	12	119.3 ± 1.8 (5.1) 51.7%	76.2 ± 0.7 (3.2) 33.0%	69.4 ± 1.1 (5.5) 30.1%	75.0 ± 1.0 (4.8) 32.5%	94.2 ± 1.5 [9]	4.5 ± 1.2 [8]	159.6 ± 1.7 (3.7) 68.7%
	2–7	**32**	**108.7 ± 2.1** **(11.3) 50.3%**	**72.7 ± 0.8** **(6.5) 33.7%**	**63.6 ± 1.4** **(12.8) 29.5%**	**68.9 ± 1.4** **(11.5) 31.9%**	**86.7 ± 1.8 [21]**	**1.6 ± 0.6 [24]**	**146.3 ± 2.7** **(10.5) 67.6%**
Adult	8	7	124.4 ± 2.7 (5.8) 52.5%	77.4 ± 1.2 (4.1) 32.7%	71.6 ± 1.4 (5.2) 30.3%	77.9 ± 1.5 (5.0) 32.9%	100.1 ± 3.3	5.4 ± 0.7 [4]	168.1 ± 3.5 [6] (5.1) 70.5%
	9	5	125.0 ± 3.5 [4] (5.5) 51.9%	76.7 ± 1.0 [4] (2.5) 31.9%	71.8 ± 0.7 (2.2) 29.6%	78.8 ± 1.3 [4] (3.3) 32.5%	101.8 ± 5.3	6.0 ± 1.6 [3]	168.8 ± 1.1 (1.4) 69.7%
	10	5	134.3 ± 4.4 (7.4) 54.1%	78.6 ± 2.6 (7.3) 31.7%	74.0 ± 1.7 (5.3) 29.8%	82.1 ± 2.0 (5.5) 33.1%	108.0 ± 6.8	9.2 ± 1.3	177.0 ± 6.0 (7.6) 71.3%
	8–10	**17**	**127.6 ± 2.2 [16]** **(6.9) 52.9%**	**77.6 ± 0.9 [16]** **(4.8) 32.0%**	**72.4 ± 0.8** **(4.5) 29.9%**	**79.4 ± 1.0 [16]** **(5.1) 32.9%**	**103.5 ± 2.8**	**7.1 ± 0.8 [12]**	**171.1 ± 24 [16]** **(5.6) 70.5%**
	≥ 12	12	139.4 ± 2.2 [11] (5.0) 55.3%	80.4 ± 0.9 [11] (3.5) 31.8%	78.2 ± 1.1 (4.6) 30.9%	85.6 ± 1.1 (4.4) 33.8%	115.5 ± 1.0 [11]	8.2 ± 0.8 [9]	175.1 ± 3.9 (7.7) 70.2%
Total		**63**	**61**	**61**	**63**	**62**	**50**	**47**	**62**
Mean for males ≥ 200 cm [max. value in brackets][b]			139.7 ± 4.5 [149.7]	84.2 ± 1.8 [87.4]	80.8 ± 2.9 [88.3]	89.0 ± 3.2 [96.6]	116.4 ± 4.8 [126.2]	6.5 ± 1.2 [12.0]	184.1 ± 6.1 [194.1]
Growth pattern, Evidence of a SGS[c]			Somatic, 17% 10 y (strong)	Neural, 5% No	Somatic, 13% No	Somatic, 19% No	Somatic, 23% 10 y (weak)	Somatic, 82% (see text)	Somatic, 10% No

Variables: P22 mastoid breadth; **P23** basion to bend of pterygoid; **L24** gnathion to anterior of foramen infraorbital; **L25** gnathion to hind border of preorbital process; **L26** height of skull at bottom of mastoid; **L27** height of sagittal crest; **M28** length of mandible.

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growth pattern. Overall growth scaled with a very weak positive slope (*b* = 1.07, 1.06) relative to CBL, increasing by 70% and 61% at 10 y (RTY), respectively.

Length of upper PC tooth row (P11) followed a somatic, monophasic growth pattern. Overall growth scaled with negative slope (*b* = 0.84) relative to CBL, increasing by 46% at 10 y (RTY).

Greatest bicanine breadth (P12) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 51% at 10 y (RTY). There was some evidence of a very slight secondary growth spurt at 10 y, but this may have been an effect of sampling.

Breadth of palate at PC 1 (P15), 3 (P16) and 5 (P17) followed a somatic growth pattern, increasing by 89%, 47% and 72% at 10 y (RTY), respectively. Overall growth expressed strong positive allometry for breadth at PC1; positive allometry for PC5; and isometry for breadth at PC3, relative to CBL. There was some evidence of a very slight secondary growth spurt in breadth at PC5 at 10 y, but this may have been an effect of sampling. The ratio of palatal breadth at PC5 (P17) to palatal length (P10) was 1 : 3 in both yearlings and adults (10 y).

Mandible (M28, M29, M30, M31, M32)

Length of mandible (M28) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope (*b* = 1.22) relative to CBL, increasing by 79% at 10 y (RTY).

Length of mandibular tooth row (M29) and length of lower post-canine row (M30) followed a neural

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Age group	Age (y)	*n*[a]	M29	M30	M31	M32
Yearling	1	2	46.8 ± 1.5 (4.5) 28.8%	37.4 [1*] (–) 23.8%	25.9 [1*] (–) 16.5%	28.3 [1*] (–) 18.0%
Subadult	2	2	50.9 ± 1.0 (2.8) 29.2%	35.9 ± 0.1 (0.4) 20.6%	29.1 ± 3.3 (15.8) 16.7%	32.0 ± 1.4 (6.0) 18.3%
	3	2	54.3 ± 1.2 (3.1) 28.5%	39.4 ± 0.8 (2.7) 20.6%	35.6 ± 2.4 (9.3) 17.1%	38.4 ± 1.8 (6.6) 18.8%
	4	8	59.3 ± 2.4 (11.6) 28.9%	39.4 ± 1.1 [6] (6.7) 19.5%	38.4 ± 1.9 [7] (12.8) 18.7%	40.5 ± 2.1 [7] (13.9) 18.7%
	5	4	61.3 ± 1.0 [3] (2.9) 28.8%	42.5 ± 0.8 (4.0) 19.6%	41.7 ± 2.1 (9.9) 19.2%	45.7 ± 1.4 (6.1) 21.1%
	6	4	61.3 ± 1.4 [3] (4.6) 27.6%	43.5 ± 0.7 (3.9) 19.6%	44.2 ± 1.5 (7.7) 20.4%	46.2 ± 1.3 (6.5) 21.2%
	7	12	67.5 ± 0.6 (3.2) 29.0%	45.4 ± 0.4 (2.9) 19.5%	48.2 ± 0.9 (6.5) 20.8%	49.3 ± 0.9 (6.3) 21.3%
	2–7	**32**	**62.1 ± 1.1 [30]** **(10.2) 28.9%**	**42.5 ± 0.6 [30]** **(8.0) 19.6%**	**42.6 ± 1.2 [31]** **(15.6) 19.7%**	**44.7 ± 1.1 [31]** **(13.7) 20.7%**
Adult	8	7	70.0 ± 1.0 (3.7) 29.6%	46.7 ± 0.8 (4.3) 19.7%	54.2 ± 1.9 (9.5) 22.9%	54.4 ± 1.9 (9.2) 23.0%
	9	5	67.4 ± 0.6 (1.9) 27.8%	46.6 ± 0.7 (3.3) 19.3%	53.7 ± 2.1 (8.8) 22.2%	53.2 ± 1.4 (5.8) 22.0%
	10	5	69.7 ± 1.8 [4] (5.1) 28.4%	46.3 ± 1.2 (5.7) 18.6%	59.5 ± 3.8 (14.2) 24.0%	58.0 ± 3.8 [4] (13.0) 23.4%
	8–10	**17**	**69.1 ± 0.7 [16]** **(3.9) 28.7%**	**46.6 ± 0.5** **(4.2) 19.3%**	**55.6 ± 1.5** **(11.4) 23.0%**	**54.9 ± 1.3 [16]** **(9.5) 22.8%**
	≥ 12	12	67.9 ± 2.0 [8] (8.4) 27.8%	46.6 ± 1.1 [11] (7.9) 18.6%	61.7 ± 2.4 (13.4) 25.0%	61.7 ± 1.9 (10.6) 24.6%
Total		**63**	**56**	**59**	**61**	**60**
Mean for males ≥ 200 cm [max. value in brackets][b]			75.4 ± 8.1 [83.5]	47.0 ± 1.3 [52.5]	62.2 ± 3.5 [68.8]	65.8 ± 1.6 [69.0]
Growth pattern, Evidence of a SGS[c]			Neural, 0.6% No	Neural, 3% No	Somatic, 28% 10 y (weak)	Somatic, 25% 10 y (weak)

Variables: M29 length of mandibular tooth row; **M30** length of lower postcanine row; **M31** height of mandible at meatus; **M32** angularis to coronoideus.

Skull variable expressed as a percentage of skull length = skull measurement (mm)/CBL(mm) × 100% (only paired samples analysed).

[a] Number of skulls for canine aged and known-aged animals. Sample size given in square brackets where this does not equal total sample size.

[b] Mean value of variable ± S.E. for the 4 largest males (≥ 200 cm) of unknown-age; maximum value in brackets.

[c] For classification of growth patterns (somatic or neural) see materials and methods; SGS, secondary growth spurt.

* S.E. of one measurement can not be measured.

** L26 and L27 were difficult to measure accurately.

Table 4.4 ***Growth in mean condylobasal length relative to mean standard body length***

Age group	Age (y)	*n*[a]	Mean CBL[b] (mm)	Mean SBL[c] (cm)	CBL rel. to SBL[d]
Yearling	1	2	159.7 ± 2.6	82.5 ± 2.5	19.4%
Subadult	2	2	174.5 ± 7.2	94.5 ± 4.5	18.5%
	3	2	196.2 ± 1.8	121.0 ± 3.0	16.2%
	4	8	205.2 ± 4.7	126.0 ± 5.2	16.3%
	5	4	219.3 ± 5.1 [3]	141.0 ± 3.8 [3]	15.6% [3]
	6	4	220.6 ± 3.4	149.0 ± 1.7	14.8%
	7	12	232.0 ± 2.5 [9]	159.0 ± 3.4 [9]	14.6% [9]
	2–7	**32**	**214.7 ± 3.6 [28]**	**138.9 ± 4.1 [28]**	**15.5% [28]**
Adult	8	7	238.8 ± 6.0 [5]	170.4 ± 7.6 [5]	14.0% [5]
	9	5	242.7 ± 2.0 [4]	170.8 ± 2.3 [4]	14.2% [4]
	10	5	248.2 ± 4.7	187.4 ± 6.5	13.2%
	8–10	**17**	**243.3 ± 2.8 [14]**	**176.6 ± 4.0 [14]**	**13.8% [14]**
	≥ 12	12	250.4 ± 4.5 [11]	183.7 ± 5.8 [11]	13.6% [11]
Total		**63**	**55**	**55**	**55**

[a] Number of skulls from canine aged and known-age animals with both CBL and SBL recorded. Of the 63 aged animals, SBL was not recorded for 8 animals, i.e., *n* = 55. Sample size given in square brackets where this does not equal total sample size.

[b] Condylobasal length (mean ± S.E.).

[c] Standard body length (mean ± S.E.). SBL is defined as the length from the nose to the tail in a straight line with the animal on its back.

[d] CBL (mm)/SBL (mm) × 100%.

growth pattern, with most growth completed by 7 y (68 mm; 45 mm). Growth was negatively allometric relative to CBL (Fig. 4.9). The ratio of the length of the lower PC row (M30) to upper PC row (P11) was 1 : 1.1 (yearlings) and 1 : 1.3 (10 y).

Height of mandible at meatus (M31), and angularis to coronoideus (M32), followed a somatic growth pattern, with a weak secondary growth spurt at 10 y. Overall growth expressed strong positive allometry relative to CBL (Fig. 4.10), with variables increasing by 130% and 105% at 10 y (RTY), respectively. Growth in vertical height of the mandible was considerably greater than that of length.

Table 4.5 ***Discriminant analysis for seal age group (subadult, adult) inferred from skull length***

Known age group		**Classification into age group** 1	2
	n[a]	Subadult (1 y 7 mo to 7 y 6 mo)	Adult[b] (≥ 7 y 7 mo)
1	**32**	26 (81%)	3
2	**29**	6	26 (90%)
Total	**61**	**32**	**29**

[a] Number of seals of known-age (MCM animals tagged as pups), and aged from counts of incremental lines observed in the dentine of upper canines (PEM animals). Yearlings excluded, i.e., n = 61. Percentage of animals correctly classified into age group is given in brackets.

[b] Included animals ≥ 12 y.

Abnormalities

Of the 60 PEM skulls examined, 14 (23%) had a cleft palate varying in severity from slight clefts to moderate deformity (PEM: 951, 958, 1453, 1560, 1882, 2050, 2051, 2052, 2053, 2132, 2137, 2141, 2197, 2253), and abnormal bony deposits were observed on the occipital bone, at the base of the parietal in PEM2049. In addition, it was clear that the deciduous canines persist in some animals until their tenth month (i.e., AP4999). According to Rand (1950): (i) deciduous canines are lost by the end of March; (ii) permanent canines do not erupt from the gums before 4 mo of age and are well developed by 8 mo (end of July).

Table 4.6 *Suture index for male Cape fur seals according to age (y) and age group*

No[a]	**Suture**[b]	**Yearling**	**Subadults**						**Adults**			
		10 mo	2 y	3 y	4 y	5 y	6 y	7 y	8 y	9 y	10 y	≥12 y
viii	**Basioccipito-basisphenoid** (brain case)	1	1	**4**	**1*–4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**
i	**Occipito-parietal** (brain case)	1	1	3	**2–4**	**4**	**3–4**	**4**	**3–4**	**4**	**4**	**4**
ii	**Interparietal** (brain case)	1	1	1	1–2	1–2	1–3	**1–4**	**1–4**	**2–4**	**3**	**3–4**
iii	**Coronal** (brain case)	1	1–2	2	1–3	1–2	2–3	1–3	1–3	1–3	3	**3–4**
x	**Squamosal-jugal** (face-zygomatic)	1	1	1	1	1	1	1	1–2	1	2	**3–4**
vi	**Premaxillary-maxillary** (face-maxilla)	1	1	1	1	1	1	1	1	1	1	1–3
xi	**Maxillary** (face-maxilla)	1	1	1	1	1	1	1	1	1	1	1–3
ix	**Squamosal-parietal** (brain case)	1	1	1	1	1	1	1	1	1	1	1–3
iv	**Interfrontal** (brain case)	1	1	1	1	1	1	1	1	1	1	1–2
viii	**Basisphenoid-presphenoid** (brain case)	1	1	1	1	1	1	1	1	1	1	1
v	**Internasal** (face-nasal)	1	1	1	1	1	1	1	1	1	1	1
	Suture index[c]	11	11–12	17	13–19	17–19	18–21	18–21	19–22	18–23	22	27–33
	Total no. skulls = 48	**2**	**2**	**2**	**7**	**3**	**4**	**8**	**6**	**3**	**1**	**10**

[a] Suture numbers i–xi correspond to Fig. 2.

[b] Sutures arranged in order of closure (1, suture fully open; 2, suture less than half-closed; 3, suture more than half-closed; 4, suture completely closed).

[c] Total value of the 11 cranial sutures (minimum and maximum). Note that the suture index is not necessarily the total value of each column.

Age inferred from counts of incremental lines observed in the dentine of upper canine, and from animals tagged as pups.

[*] The basioccipito-basisphenoid was fully open in one 4-y-old (AP4496).

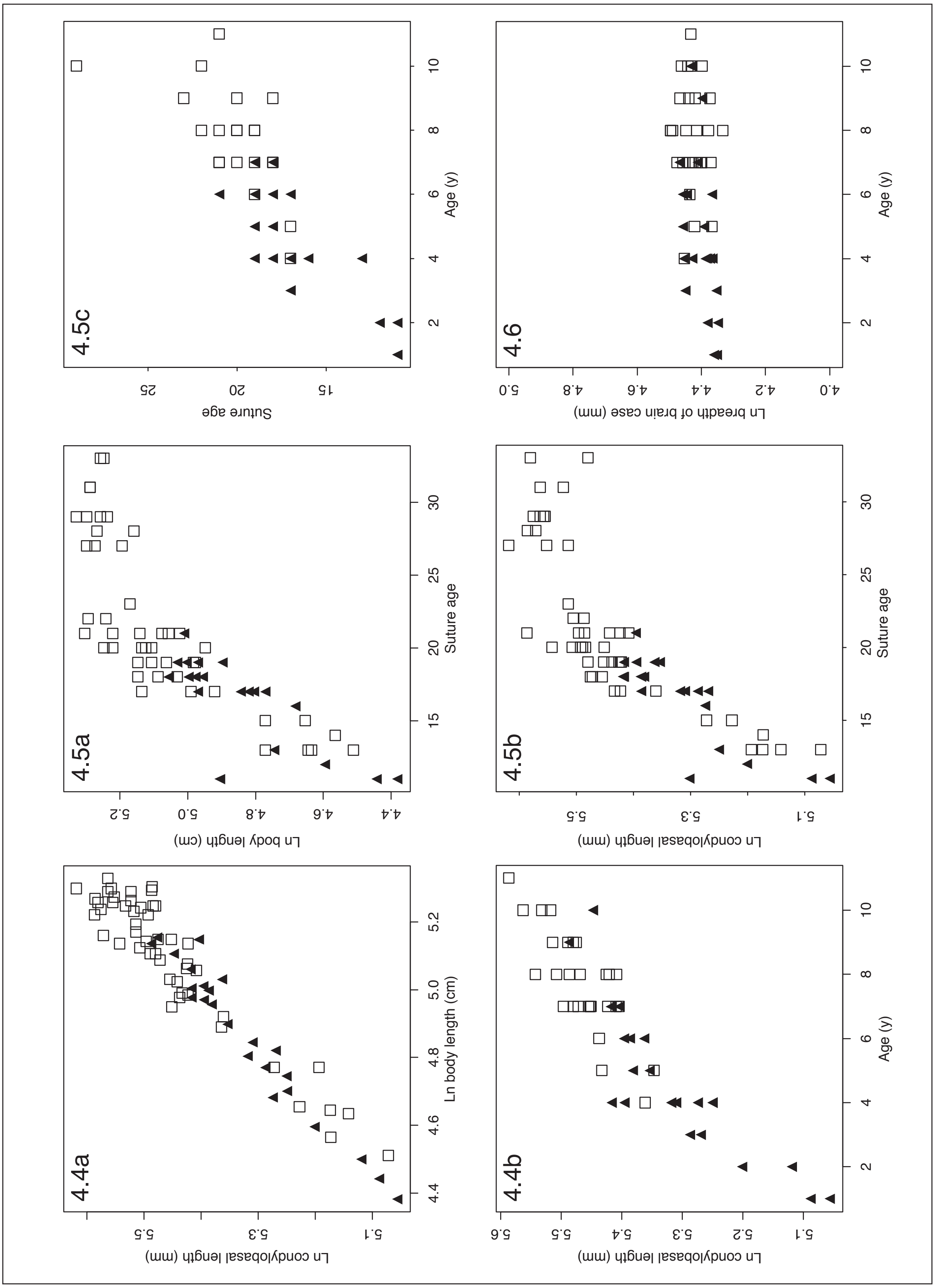

Fig. 4.4a, 4.4b Bivariate plot of log condylobasal length (mm) on: (a) log body length (cm) and (b) age (y).

Fig. 4.5a, 4.5b, 4.5c Bivariate plots of: (a) log body length (cm) on suture age; (b) log condylobasal length (mm) on suture age; (c) suture age on age (y).

Fig. 4.6 Example of neural growth. Log breadth of brain case (mm) on age (y).
Solid triangles, known-age animals (MCM). Squares, canine aged animals (PEM).

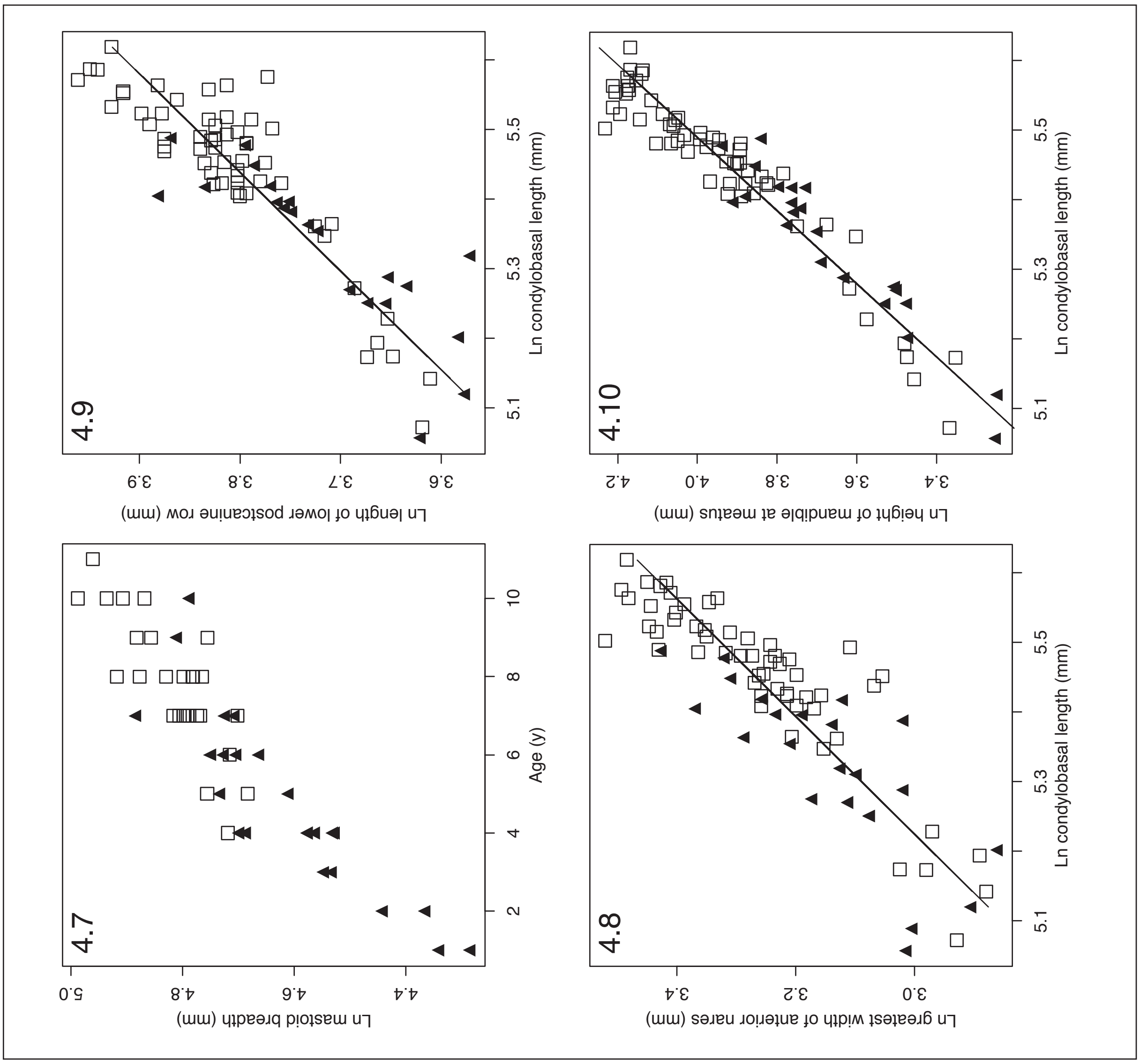

Fig. 4.7 Example of somatic, biphasic growth. Log mastoid breadth (mm) on age (y).
Fig. 4.8 Example of isometric growth. Log greatest width of anterior nares on log condylobasal length (mm).
Fig. 4.9 Example of negative allometry. Log length of lower postcanine row (mm) on log condylobasal length (mm).
Fig. 4.10 Example of strong positive allometry. Log height of mandible at meatus (mm) on log condylobasal length (mm).
Solid triangles, known-age animals (MCM). Squares, canine aged animals (PEM).

DISCUSSION

Skull size

Arctocephalus pusillus is the largest of the fur seals, therefore the skull is correspondingly large. In the present study, the maximum CBL was 275.4 mm (PEM898); however, skulls up to 307 mm (Australian fur seal, *A. p. doriferus*) have been reported (Cruwys & Friday, 1995). As with all southern fur seals, the skull is considerably larger in males than in females, reflecting pronounced sexual dimorphism (see Stewardson *et al.*, 200X*b*).

East coast and west coast animals

It has been suggested that marine mammal species inhabiting warmer waters may be smaller in body size than marine mammal species inhabiting cooler waters (Ross & Cockcroft, 1990). Long-term climatic data in Algoa Bay, based on daily measurements, indicate that the mean water temperature is 16–17° C in winter and 21–22° C in summer. For Luderitz (near Sinclair Island), mean water temperature is 12–13° C in winter and 14–15° C in summer, considerably cooler than Eastern Cape waters (Dr M. Grundlingh, pers. comm.). When comparing CBL from adult Cape fur seals from these two geographic locations, we did not find sufficient reason to reject the hypothesis that the population means for skull length were equal using PEM animals > 12 y. However, it is not clear if this result was influenced by a larger number of older adults in the PEM sample. When younger PEM animals were included in the adult sample (7–12^{+} y), Eastern Cape seals were found to be significantly smaller than west coast seals. Further testing using a larger sample of aged animals is required.

Skull shape

Morphological observations of the skull were generally consistent with earlier studies by Rand (1949*b*, 1950, 1956) and Repenning *et al.*, (1971). As for all otariids, the frontal bones project anteriorly between the nasal bones; supraorbital processes are present; the tympanic bulla are small and flat, comprised primarily of the ectotympanic; the alisphenoid canal is present; the mastoid processes are massive; the jugal-squamosal joint of the zygomatic arch overlap; and deep transverse grooves occur on the occlusal surface of the upper incisors (Burns & Fay, 1970; King, 1983; present study).

Within the species, the forehead is convex at the supraorbital region; the snout is long; the nasals are long and flared anteriorly; the palate is moderately broad and arched; the maxillary shelf at the root of the zygomatic process is very short in an anterio-posterior direction; the tooth rows are parallel, with robust, tricuspid PC, and a slight diastema between upper PC 5 and 6 (Repenning *et al.*, 1971; present study).

As with other species of this genus, the interorbital region (D7) was less than 20% of CBL in adults (i.e., 15%); palatal notch to the incisors (P10) was more than 37% of CBL (i.e., 43%); and nasal length (D5) fell within 14% (smallest fur seal, *A. galapagoensis)* and 18% (largest fur seal, *A. pusillus*) of CBL (i.e., 18%) (Scheffer, 1958; Cruwys & Friday, 1995; present study).

Condylobasal length as an indicator of SBL and age

In male Cape fur seals, CBL continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). The absence of very old skulls of known-age (18–20 y), made it difficult to determine overall growth in CBL. In contrast CBL continues to increase until at least 13 y in male *C. ursinus* (Scheffer & Wilke, 1953, but see Scheffer & Kraus, 1964) and slows at 10 y in male *E. jubatus* (Fiscus, 1961).

Condylobasal length was found to be a reasonable indicator of SBL and age group, but not of absolute age. The classification criteria for SBL developed in this study will be particularly useful when a seal is decomposed/scavenged (total SBL can not be measured), and/or the skull is incomplete /absent (total SBL can not be extrapolated from skull length). The classification criteria for age group will be particularly useful when canines are not available for age determination; or museum records have been misplaced or destroyed. As more specimens become available, the classification criteria will be more precise.

Suture index as an indicator of age

Although cranial sutures close progressively with age, suture age was not considered to be good indicator of chronological age (y) or age group (present study). Similar observations have been made in other male otariids, e.g., in *C. ursinus,* the rate of suture closure is highly variable, and like SBL and CBL, is a poor indicator of chronological age (Scheffer & Wilke, 1953). Suture age is examined in more detail elsewhere (Stewardson *et al.*, 200X)

Function and growth

Neurocranium region

In mammals, growth of the protective brain case corresponds closely to that of the enclosed brain (Moore, 1981). The brain/brain case grows rapidly during prenatal and postnatal life; attains full size early in development before that of the basicranium or face; and scales with negative slope relative to skull size (Moore, 1966, 1981; Bryden, 1972; King, 1972; Gould, 1975; Moore & Lavelle, 1975; Enlow, 1982; Shea, 1985; Wayne, 1986; Hartwig, 1993; Morey, 1990; present study). Early maturation of the brain /brain case is essential for nervous control of the body.

The sagittal crest strengthens the skull, and provides an increased surface area for muscle attachment. In adults, large crest size is advantageous in combat behaviour between breeding bulls, and in feeding (increases bite force). Sagittal crest height begins to increase in size at 4–7 y (highly variable), reaching at least 12 mm in some adult males. In male *Z. californianus,* the sagittal crest begins to develop at 5 y, with height ranging from 11–36.5 mm in adults (Orr *et al.*, 1970). In male *E. jubatus* , sagittal crest height ranged from 7–37 mm in adults (Fiscus, 1961). Variation in crest height in older males presumably reflects differences between breeding and non-breeding bulls.

Basicranium region

The basicranium accommodates the hearing apparatus (Enlow, 1982). As with other mammals, growth of the otic capsule (and associated structures) appears to follow a neural growth pattern (Bast & Anson, 1949; Hoyte, 1961; Moore, 1981). Early development of the otic capsule enables juveniles to recognise the ‘pup-attraction call’ of their mothers. Mother-pup recognition is critical for pinnipeds living within a colony where separation is frequent, and mother-pup pairs are numerous (see Rand, 1967; Trillminch, 1981; Oftedal *et al.*, 1987; Bowen, 1991).

Unlike the otic capsule, calvarial breadth and mastoid breadth mature much later in life (present study). In adults, enlarged mastoids are advantageous in combat behaviour between breeding bulls, and in feeding (large head size/increases bite force); and facilitate directional hearing (provides a greater surface area of specific orientation for selective reflection of sound) (Repenning, 1972).

Frontal region

The interorbital region provides the structural base for the snout (Enlow, 1982). The dimensions of this region increase with age to accommodate the development of the proportionally large snout.

The supraorbital processes strengthen the skull (very thick in adults), protects the orbital region, and increases bite force. In adults seals, this enlarged structure is advantageous in feeding, and in combat behaviour between breeding bulls.

Zygomatic arch

The zygomatic arch protects the eye, provides a base for the masseter and part of the temporal muscle, accommodates conductive hearing (squamous root) and is the point of articulation for the mandible (Evans, 1993; Repenning, 1972). As with other mammals, the zygomatic arch enlarges laterally and inferiorly to accommodate enlargement of the head, and a correspondingly greater temporal muscle mass (Moore, 1981; present study).

The orbital border of the zygomatic bone forms the ventral margin of the eye socket. As with other pinnipeds, the orbits were large to accommodate large eyes (King, 1972). In Cape fur seals, the horizontal diameter of the eye is *c.* 40 mm (e.g., animals AP5215, 2 y 4 mo; AP5210, 3 y). Although large eyes are potentially advantageous in the detection of benthic and/or fast moving pelagic prey (David, 1987), vision is not necessary to locate/capture prey (see King, 1983).

Splanchnocranium region

In Cape fur seals, lateral face length and width of snout at the canines, scaled with positive slope relative to CBL, similar to that of wild canids (Lumer, 1940; Morey, 1990). As the face and snout increased in length, the brain case and orbits became proportionally smaller.

In mammals, the size and shape of the brain establishes boundaries that determine the amount of facial growth; and special sense organs housed within the face influence the direction of growth (Enlow, 1982). In adult Cape fur seals, the brain is relatively large and more spherical than in terrestrial carnivores (Harrison & Kooyman, 1968; King, 1983), yet long and narrow compared to humans (i.e., small cerebrum). Therefore, the snout is correspondingly long and narrow. The wide nasal openings were aligned in a horizontal plane with the nerves of the olfactory bulb; and the orbital axis is pointed straight forward in the direction of body movement (Enlow, 1982; present study).

Nasal and palatal region

The naso-maxillary complex is the facial part of the respiratory (nasal cavity) and alimentary (oral cavity) tracts, which also facilitates sound production and the sense of smell. The floor of the nasal cavity forms the roof of the oral cavity, thus growth of the two cavities was highly coordinated. Growth was predominantly somatic, with similar allometric trends to those of wild canids (Lumer, 1940; Wayne, 1986; Morey, 1990). Progressive growth of this region is needed to accommodate the large dental battery.

Growth of dentition has been described by Rand (1950, 1956). At 6 to 12 mo, Cape fur seals gradually transfer from milk to solids (fish, crustacean and cephalopod) (Warneke & Shaughnessy, 1985). Although the small, deciduous teeth are usually lost by the end of the first 5 mo (Rand, 1956), deciduous canines may persist for 10 mo (present study). The permanent teeth are used to hold slippery prey (gripping), and to reduce prey size (biting and shearing). Growth of the permanent teeth is a gradual process, with diet becoming more varied with age and experience (Rand, 1959). In the upper jaw, the canines protrude beyond the tip of the 3rd upper incisor only in the 2nd y (Rand, 1956).

In male Cape fur seals, the ability to produce sound is evident at birth, with vocal skills broadening with increased age (Rand, 1967). In otariids, the production of sound is important in mother-pup recognition; communicating within a colony; and affirmation of territorial boundaries and social status (e.g., Stirling & Warneke, 1971).

Although the olfactory area is reduced when compared to terrestrial carnivores, the sense of smell appears to be well developed, and plays an important role in the detection of sexually receptive females, and land predators (Harrison & Kooyman, 1968; Peterson, 1968; King, 1983; Renouf, 1991; Wartzok, 1991).

Mandible

Using human anatomy as a model, the horizontal part of the mandible (corpus) provides the structural basis for tooth formation, and the vertical part (ramus = condyle, angular process, coronoid process, masseteric fossa) provides areas for articulation and muscle attachment.

As with other carnivores, the ramus increased substantially in height to accommodate implantation of the teeth, and expansion of the nasal region (Evans, 1993; Enlow, 1982; present study). The coronoid process grew upwards and backwards increasing in thickness on the anterior borders; the condyles grew backwards, beyond the level of the coronoid process; and the masseteric fossa formed a large, deep depression for jaw muscle (masseter and temporalis) attachment. Large jaws and jaw muscles are advantageous in feeding and in combat behaviour between breeding bulls (increases bite force/increases gape).

In mammals, the mandible of newborns is proportionally smaller than the upper jaw, and therefore must grow at a slightly faster rate to provide anatomical balance (Enlow, 1982). In order to achieve correct occlusal relationships between upper and lower dentition, the rate of growth between the mandible and maxilla needs to be highly coordinated (Moore, 1981). In Cape fur seals, the PC teeth are robust, therefore the tooth row is long.

Growth rate of the lower PC row (b = 0.7) was similar to that of the upper PC row (b = 0.8), relative to CBL. Overall percent increase in growth was greater in the upper jaw because there are 6 PC in the upper jaw and only 5 in the lower jaw. The ratio of length of the lower PC row to upper PC row was 1 : 1.1 in yearlings, and increased to 1 : 1.3 in adults (at 10 y). Growth of the anterior dentition was considerably greater than that of the PC, due to development of the large canines.

CONCLUSION

Information presented in this study confirms earlier descriptions of the Cape fur seal skull (Rand, 1949*b*, 1950, 1956; Repenning *et al*., 1971), and provides new information on skull growth according to age (y). In male Cape fur seals, CBL continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). Growth of the skull was a differential process and not simply an enlargement of overall size. Components within each region matured at different rates and grew in different directions. Apart from the dentition, all variables of the facial skeleton followed a somatic growth trajectory, and most variables were positively allometric with CBL. Breadth of braincase and basion to bend of pterygoid followed a neural growth trajectory and scaled with negative slope relative to CBL. Condylobasal length and suture age were found to be poor indicators of absolute age. However, CBL was a reasonable indicator of SBL and age group.

Further information is needed on cranial capacity; orbital size; tooth erruption; and the development of the sagittal crest in relation to chronological age and social status. Meaningful biological, evolutionary and functional inferences on skull growth can only be made when similar data is available for other pinniped species of known-age. Multivariate statistical procedures can then be employed to summarise morphometric relationships within and among populations.

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Appendix 4.1 ***Cape fur seals (n = 83) examined in this study.*** **Animals were collected from the coast of southern Africa between December 1982 and July 1997.**

	ID No.	Date of collection	Approximate location[a]	Region[b]	Method of collection[c]	SBL (cm)
1.	PEM898	22 Dec 82	1 km E of Van Starden's River Mouth, St. Francis Bay (FB)	ECP	stranding	200
2.	PEM916	Jan 1983	Willows, Port Elizabeth (PE) (34° 03'S, 25° 35'E)	ECP	stranding	91
3.	PEM917	11 Jan 83	2 km W of Maitland River Mouth, FB	ECP	stranding	104
4.	PEM951	16 May 83	35 km E of Sundays River Mouth, Woody Cape (WC)	ECP	stranding	170
5.	PEM958	13 Dec 83	Humewood, PE (33° 59'S, 25° 40'E)	ECP	other	190
6.	PEM975	7 Oct 83	40 km E of Sundays River Mouth, WC	ECP	stranding	172
7.	PEM1073	12 Sep 84	Oyster Bay (34° 10'S, 24° 39'E)	ECP	stranding	133
8.	PEM1453	30 Jan 88	3 km E Kabeljous River Mouth, Jeffreys Bay	ECP	stranding	193
9.	PEM1507	5 Feb 88	Kings Beach, PE (33° 58'S, 25° 39'E)	ECP	stranding	198
10.	PEM1560	26 Oct 88	Seaview (34° 01'E, 25° 17'S)	ECP	stranding	201
11.	PEM1587	18 May 89	Amsterdamhoek (33° 52'S, 25° 38'E)	ECP	stranding	192
12.	PEM1698	12 Apr 90	25 km E of Sundays River Mouth (WC)	ECP	stranding	190
13.	PEM1704	19 June 90	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	NR	147
14.	PEM1868	24 Sep 91	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	199
15.	PEM1877	2 Apr 92	Lauries Park, PE (34° 02'S, 25° 23'E)	ECP	stranding	185
16.	PEM1879	13 Apr 92	Flat Rocks, PE (34° 00'S, 25° 42'E)	ECP	stranding	200
17.	PEM1882	6 May 92	King's Beach, PE (33° 58'S, 25° 39'E)	ECP	stranding	180
18.	PEM1890	13 July 92	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	192
19.	PEM1891	18 July 92	Hobie Beach, SE of King's Beach (33° 58'S, 25° 39'E)	ECP	rehab. (D)	137
20.	PEM1892	27 July 92	Sardinia Bay (34° 02'S, 25° 29'E), 800 m E of boat shed	ECP	stranding	185
21.	PEM1895	29 July 92	Cape Recife, PE (34° 02'S, 25° 42'E), 2 km E of lighthouse	ECP	stranding	188
22.	PEM2004	25 July 92	EC trawl grounds (34° 45'S, 24° 18'E–34° 48'S, 24° 00'E)	ECP	by-catch	–
23.	PEM2006	13 Aug 92	EC trawl grounds (34° 45'S, 24° 25'E–34° 42'S, 24° 40'E)	ECP	by-catch	–
24.	PEM2007	14 Aug 92	EC trawl grounds (34° 42'S, 24° 51'E–34° 42'S, 24° 42'E)	ECP	by-catch	–
25.	PEM2008	14 Aug 92	EC trawl grounds (34° 41'S, 24° 42'E–34° 38'S, 24° 54'E)	ECP	by-catch	–
26.	PEM2009	22 Aug 92	EC trawl grounds (34° 41'S, 24° 45'E–34° 37'S, 24° 59'E)	ECP	by-catch	–
27.	PEM2010	22 Aug 92	EC trawl grounds (34° 47'S, 24° 11'E–34° 46'S, 24° 25'E)	ECP	by-catch	–
28.	PEM2013	14 Sep 92	EC trawl grounds (34° 24'S, 25° 50'E–34° 25'S, 26° 02'E)	ECP	by-catch	–
29.	PEM2014	25 Sep 92	EC trawl grounds (34° 23'S, 26° 04'E–34° 23'S, 25° 58'E)	ECP	by-catch	–
30.	PEM2035	11 Mar 93	The Pipes, SE of Pollock Beach (33° 59'20"S, 25° 40' 30"E)	ECP	stranding	118
31.	PEM2036	19 Mar 93	Black Rocks, Algoa Bay (AB) (33° 50'S, 26° 15'E)	ECP	stranding	–
32.	PEM2044	28 May 93	Seaview (34° 01'S, 25° 17'E), Otter Pools	ECP	stranding	206
33.	PEM2045	30 May 93	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	145
34.	PEM2046	19 May 93	EC trawl grounds (35° 09'S, 21° 28'E)	ECP	by-catch	141
35.	PEM2048	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	ECP	by-catch	157
36.	PEM2049	7 June 93	Kini Bay, Western Beach (34° 01'S, 25° 26'E)	ECP	stranding	174
37.	PEM2050	8 June 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	ECP	stranding	165
38.	PEM2051	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	ECP	by-catch	168
39.	PEM2052	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	ECP	by-catch	171
40.	PEM2053	28 June 93	EC trawl grounds (34° 46'S, 24° 21'E–34° 44'S, 24° 32'E)	ECP	by-catch	153
41.	PEM2054	29 June 93	EC trawl grounds (34° 45'S, 24° 28'E–34° 47'S, 24° 18'E)	ECP	by-catch	165
42.	PEM2081	19 July 93	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	162
43.	PEM2082	July 93	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	176
44.	PEM2087	17 Aug 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	ECP	stranding	190
45.	PEM2132	20 Dec 93	Woody Cape, AB (33° 46'S, 26° 19'E)	ECP	stranding	195
46.	PEM2137	5 Jan 94	Summerstrand, PE (34° 00'S, 25° 42'E)	ECP	rehab. (D)	118
47.	PEM2140	17 Jan 94	40 km E of Sundays River Mouth, WC	ECP	stranding	187
48.	PEM2141	17 Jan 94	39 km E of Sundays River Mouth, WC	ECP	stranding	198
49.	PEM2143	21 Jan 94	Seaview (34° 01'S, 25° 17'E)	ECP	stranding	189
50.	PEM2151	3 Feb 94	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	194
51.	PEM2197	12 July 94	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	160
52.	PEM2198	July 94	Plettenberg Bay (34° 03'S, 23° 24'E)	ECP	stranding	105
53.	PEM2201	5 July 94	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	103
54.	PEM2238	July 1994	Durban (29° 50'S, 31° 00'E)	–[d]	rehab. (D)	96
55.	PEM2248	12 Aug 94	Seaview (34° 01'S, 25° 27'E)	ECP	stranding	158
56.	PEM2252	22 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	172
57.	PEM2253	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	152
58.	PEM2254	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	146
59.	PEM2257B	8 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	170
60.	MCM1565	25 Sep 84	2 miles offshore the Vondeling area (33° 18'S, 18° 06'E)	WC	sci. permit	118

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	ID No.	**Date of collection**	**Approximate location**[a]	**Region**[b]	**Method of collection**[c]	**SBL (cm)**
61.	MCM1786	30 Sep 94	St Helena Bay	WC	stranding	85
62.	MCM1809	14 Nov 84	Kleinzee	WC	sci. permit	173
63.	MCM1810	12 Feb 84	Kleinzee	WC	sci. permit	172
64.	MCM2763	10 Feb 85	Doringbaai area (31° 30'S, 16° 30'E)	WC	by-catch	127
65.	MCM2795	27 July 88	Demersal fishing grid 502	SWC	by-catch	158
66.	MCM3582	6 June 86	Offshore Dassen Island (33° 21'S, 17° 40'E)	WC	by-catch	142
67.	MCM3586	22 Apr 86	8 miles off Wilderness	SC	by-catch	144
68.	MCM3587	5 June 86	25 nm west of Mossel Bay	SC	by-catch	145
69.	MCM3636	17 July 87	West of Dassen Island (37° 45'S, 17° 35'E)	WC	by-catch	148
70.	MCM4365	13 Mar 90	3.5 nm off Gouritz River Mouth (34° 23'S, 21° 51'E)	SC	by-catch	124
71.	MCM4388	23 Oct 90	20 nm south of Gouritz River Mouth (34° 26'S, 21° 53'E)	SC	by-catch	122
72.	MCM4577	17 Jan 94	Cape Town Harbour	WC	stranding	150
73.	MCM4595	17 Oct 95	Off Cape Point (34° 45'S, 21° 49'E)	SW	by-catch	134
74.	MCM4597	15 Sep 95	South of Dassen Island (33° 30'S, 17° 40'E)	WC	by-catch	170
75.	MCM4989	14 Aug 96	St Helena	WC	by-catch	99
76.	MCM4992	13 Sep 96	Demersal fishing grid 493 (35° 30'S, 18° 56'E)	SW	by-catch	165
77.	MCM4996	28 Sep 96	Offshore Saldahna Bay (33° 10'S, 17° 14'E)	WC	by-catch	115
78.	MCM4999	10 July 96	Seal Island, St Helena Bay	WC	by-catch	80
79.	MCM5002	10 Jun 96	Offshore Saldahna Bay (33° 16'S, 17° 07'E)	WC	by-catch	108
80.	MCM5133	14 Jan 97	Offshore Plettenberg Bay (34° 30'S, 23° 30'E)	ECP	by-catch	153
81.	MCM5135	23 July 97	Offshore Stompneus Lighthouse	WC	stranding	110
82.	MCM5136	15 July 97	Offshore St Helena Bay (32° 27'S, 17° 38'E)	WC	by-catch	149
83.	MCM5145	Nov 94	St Helena Bay	WC	by-catch	90

[a] Kabeljous River Mouth (34° 00'S, 24° 56'E); Maitland River Mouth (33° 59'S, 25° 18'E); Sundays River Mouth (33° 43'S, 25° 51'E); and Van Starden's River Mouth (33° 58'S, 25° 13'E).

[b] WC (west coast), north of Cape Point Lighthouse (34° 21'S, 18° 29'E); SWC (south west coast), south of Cape Point Lighthouse to Cape Agulhas (34° 50'S, 20° 00'E); SC (south coast), east of Cape Agulhas, but excluding the Eastern Cape; and ECP (Eastern Cape Province), Plettenberg Bay (34˚ 03'S, 23˚ 24'E) to East London (33˚ 03'S, 27˚ 54'E).

[c] Stranding, animal washed up dead on beach (*n* = 38). By-catch, animal incidentally caught in a commercial trawl net during fishing operations (*n* = 37). Sci. permit, animal collected under scientific permit or harvested (*n* = 3). Rehab. (D), animal died during rehabilitation at the Port Elizabeth Oceanarium (*n* = 3). Other, animal died from other causes (*n* = 1, PEM958 found floating in the ocean off Humewood beach).

[d] Animal PEM2238 collected NE of the Eastern Cape, i.e., Durban (29° 50'S, 31° 00'E).

NR. not recorded.

Appendix 4.2 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on log length of seal***

Dependent variable	**Linear regression**				**Allometry**		
	n[a]	**Intercept ± S.E.**	**Slope ± S.E.**	***r*** **(*p*)**	**Alternative hypothesis**	***d.f.***	***p***
Dorsal							
D1 Condylobasal length	74	2.65 ± 0.08	0.55 ± 0.02	0.93 (0.00)	$H_1: \hat{\beta} < 1$	72	0.00
D2 Gnathion to middle of occipital crest	73	2.51 ± 0.11	0.55 ± 0.02	0.93 (0.00)	NA	NA	NA
D3 Gnathion to posterior end of nasals	71	1.12 ± 0.12	0.65 ± 0.02	0.92 (0.00)	NA	NA	NA
D4 Greatest width of anterior nares	71	0.16 ± 0.19	0.61 ± 0.04	0.88 (0.00)	$H_1: \hat{\beta} < 1$	69	0.00
D5 Greatest length of nasals	70	0.19 ± 0.20	0.69 ± 0.04	0.85 (0.00)	$H_1: \hat{\beta} < 1$	69	0.00
D6 Breadth at preorbital processes	69	0.85 ± 0.13	0.65 ± 0.03	0.90 (0.00)	NA	NA	NA
D7 Least interorbital constriction	69	-0.04 ± 0.16	0.70 ± 0.03	0.88 (0.00)	$H_1: \hat{\beta} < 1$	67	0.00
D8 Breadth at supraorbital processes	65	1.07 ± 0.18	0.57 ± 0.04	0.86 (0.00)	$H_1: \hat{\beta} < 1$	63	0.00
D9 Breadth of brain case	71	3.95 ± 0.09	0.10 ± 0.02	0.40 (0.00)	NA	NA	NA
Palatal							
P10 Palatal notch to incisors	73	1.56 ± 0.15	0.60 ± 0.03	0.86 (0.00)	$H_1: \hat{\beta} < 1$	71	0.00
P11 Length of upper postcanine row	73	1.70 ± 0.15	0.46 ± 0.03	0.77 (0.00)	NA	NA	NA
P12 Greatest bicanine breadth	73	0.58 ± 0.16	0.64 ± 0.03	0.92 (0.00)	$H_1: \hat{\beta} < 1$	71	0.00
P13 Gnathion to posterior end of maxilla	73	1.74 ± 0.10	0.58 ± 0.02	0.91 (0.00)	$H_1: \hat{\beta} < 1$	71	0.00
P14 Breadth of zygomatic root of maxilla	74	0.45 ± 0.27	0.44 ± 0.05	0.74 (0.00)	$H_1: \hat{\beta} < 1$	72	0.00
P15 Breadth of palate at postcanine 1	72	-1.16 ± 0.25	0.84 ± 0.05	0.89 (0.00)	$H_1: \hat{\beta} < 1$	70	0.001
P16 Breadth of palate at postcanine 3	72	0.21 ± 0.19	0.60 ± 0.04	0.87 (0.00)	$H_1: \hat{\beta} < 1$	70	0.00
P17 Breadth of palate at postcanine 5	71	-0.02 ± 0.18	0.68 ± 0.04	0.87 (0.00)	$H_1: \hat{\beta} < 1$	69	0.00
P18 Gnathion to hind border of postglenoid process	72	1.88 ± 0.08	0.65 ± 0.02	0.93 (0.00)	NA	NA	NA
P19 Bizygomatic breadth	74	1.69 ± 0.12	0.62 ± 0.02	0.91 (0.00)	NA	NA	NA
P20 Basion to zygomatic root (anterior)	72	2.36 ± 0.07	0.53 ± 0.01	0.93 (0.00)	NA	NA	NA
P21 Calvarial breadth	72	1.76 ± 0.09	0.58 ± 0.02	0.94 (0.00)	NA	NA	NA
P22 Mastoid breadth	72	1.15 ± 0.11	0.72 ± 0.02	0.93 (0.00)	NA	NA	NA
P23 Basion to bend of pterygoid	72	2.52 ± 0.08	0.36 ± 0.02	0.91 (0.00)	$H_1: \hat{\beta} < 1$	70	0.00
Lateral							
L24 Gnathion to foramen infraorbital	73	0.85 ± 0.14	0.67 ± 0.03	0.91 (0.00)	$H_1: \hat{\beta} < 1$	71	0.00
L25 Gnathion to hind border of preorbital process	73	0.89 ± 0.11	0.68 ± 0.02	0.92 (0.00)	NA	NA	NA
L26 Height of skull at bottom of mastoid	61	1.40 ± 0.20	0.63 ± 0.04	0.90 (0.00)	NA	NA	NA
L27 Height of sagittal crest	55	–	–	0.73 (0.00)	–	–	–
Mandibular							
M28 Length of mandible	74	1.58 ± 0.09	0.69 ± 0.02	0.94 (0.00)	$H_1: \hat{\beta} < 1$	72	0.00
M29 Length of mandibular tooth row	64	1.70 ± 0.12	0.49 ± 0.02	0.85 (0.00)	$H_1: \hat{\beta} < 1$	62	0.00
M30 Length of lower postcanine row	69	1.96 ± 0.11	0.36 ± 0.02	0.83 (0.00)	$H_1: \hat{\beta} < 1$	67	0.00
M31 Height of mandible at meatus	72	-1.45 ± 0.19	1.06 ± 0.04	0.93 (0.00)	$H_1: \hat{\beta} \neq 1$**	70	0.26
M32 Angularis to coronoideus	70	-0.89 ± 0.17	0.95 ± 0.03	0.94 (0.00)	$H_1: \hat{\beta} \neq 1$**	68	0.28

[a] Number of skulls from aged and unaged animals with both skull variable and SBL recorded. Of the 83 aged and unaged animals, SBL was not recorded for 9 animals, i.e., $n = 74$.

r, Spearman rank-order correlation coefficient.

NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.

** Since the p-value was > 0.05 then we cannot reject H_0 in favour of H_1 at the 5% significance level; therefore growth is isometric.

Appendix 4.3 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on log condylobasal length***

Dependent variable	**Linear regression**				**Allometry**		
	n[a]	**Intercept ± S.E.**	**Slope ± S.E.**	***r* (*p*)**	**Alternative hypothesis**	***d.f.***	***p***
Dorsal							
D2 Gnathion to middle of occipital crest	79	-0.22 ± 0.17	1.01 ± 0.03	0.97 (0.00)	NA	NA	NA
D3 Gnathion to posterior end of nasals	80	-2.01 ± 0.19	1.18 ± 0.04	0.95 (0.00)	$H_1: \hat{\beta} > 1$	78	0.00
D4 Greatest width of anterior nares	79	-2.62 ± 0.32	1.08 ± 0.06	0.87 (0.00)	$H_1: \hat{\beta} \neq 1$**	77	0.18
D5 Greatest length of nasals	78	-3.21 ± 0.31	1.27 ± 0.06	0.88 (0.00)	$H_1: \hat{\beta} > 1$	76	0.00
D6 Breadth at preorbital processes	78	-2.19 ± 0.21	1.16 ± 0.04	0.92 (0.00)	$H_1: \hat{\beta} > 1$	76	0.00
D7 Least interorbital constriction	78	-3.36 ± 0.30	1.27 ± 0.06	0.89 (0.00)	$H_1: \hat{\beta} > 1$	76	0.00
D8 Breadth at supraorbital processes	74	-1.66 ± 0.34	1.03 ± 0.06	0.83 (0.00)	NA	NA	NA
D9 Breadth of brain case	80	3.48 ± 0.19	0.17 ± 0.03	0.39 (0.00)	NA	NA	NA
Palatal							
P10 Palatal notch to incisors	82	-1.22 ± 0.20	1.07 ± 0.04	0.89 (0.00)	NA	NA	NA
P11 Length of upper postcanine row	82	-0.54 ± 0.23	0.84 ± 0.04	0.77 (0.00)	NA	NA	NA
P12 Greatest bicanine breadth	82	-2.38 ± 0.26	1.14 ± 0.05	0.93 (0.00)	$H_1: \hat{\beta} > 1$	80	0.00
P13 Gnathion to posterior end of maxilla	82	-1.06 ± 0.11	1.06 ± 0.02	0.96 (0.00)	NA	NA	NA
P14 Breadth of zygomatic root of maxilla	83	-1.97 ± 0.48	0.85 ± 0.09	0.75 (0.00)	$H_1: \hat{\beta} \neq 1$**	81	0.17
P15 Breadth of palate at postcanine 1	73	-4.89 ± 0.48	1.47 ± 0.09	0.89 (0.00)	$H_1: \hat{\beta} > 1$	71	0.00
P16 Breadth of palate at postcanine 3	73	-2.42 ± 0.35	1.04 ± 0.06	0.87 (0.00)	$H_1: \hat{\beta} \neq 1$**	71	0.56
P17 Breadth of palate at postcanine 5	80	-3.11 ± 0.34	1.20 ± 0.06	0.85 (0.00)	$H_1: \hat{\beta} > 1$	78	0.001
P18 Gnathion to hind border of postglenoid process	77	-1.18 ± 0.12	1.16 ± 0.02	0.96 (0.00)	NA	NA	NA
P19 Bizygomatic breadth	83	-1.25 ± 0.21	1.12 ± 0.04	0.89 (0.00)	NA	NA	NA
P20 Basion to zygomatic root (anterior)	81	-0.16 ± 0.08	0.96 ± 0.02	0.97 (0.00)	NA	NA	NA
P21 Calvarial breadth	81	-0.76 ± 0.16	1.00 ± 0.03	0.94 (0.00)	NA	NA	NA
P22 Mastoid breadth	81	-2.22 ± 0.17	1.29 ± 0.03	0.95 (0.00)	NA	NA	NA
P23 Basion to bend of pterygoid	81	0.89 ± 0.12	0.63 ± 0.02	0.90 (0.00)	$H_1: \hat{\beta} < 1$	79	0.00
Lateral							
L24 Gnathion to foramen infraorbital	82	-2.61 ± 0.17	1.26 ± 0.03	0.94 (0.00)	NA	NA	NA
L25 Gnathion to hind border of preorbital process	82	-2.49 ± 0.14	1.25 ± 0.03	0.97 (0.00)	NA	NA	NA
L26 Height of skull at bottom of mastoid	70	-1.90 ± 0.32	1.19 ± 0.06	0.94 (0.00)	NA	NA	NA
L27 Height of sagittal crest	60	–	–	0.80 (0.00)	–	–	–
Mandibular							
M28 Length of mandible	82	-1.58 ± 0.10	1.22 ± 0.02	0.98 (0.00)	NA	NA	NA
M29 Length of mandibular tooth row	73	-0.61 ± 0.19	0.88 ± 0.04	0.85 (0.00)	$H_1: \hat{\beta} < 1$	71	0.002
M30 Length of lower postcanine row	78	0.22 ± 0.18	0.66 ± 0.03	0.84 (0.00)	$H_1: \hat{\beta} < 1$	76	0.00
M31 Height of mandible at meatus	81	-6.31 ± 0.32	1.88 ± 0.06	0.95 (0.00)	$H_1: \hat{\beta} > 1$	79	0.00
M32 Angularis to coronoideus	79	-5.11 ± 0.28	1.66 ± 0.05	0.95 (0.00)	$H_1: \hat{\beta} > 1$	77	0.00

[a] Number of skulls from aged and unaged animals with both skull variable and CBL recorded. CBL was recorded for all animals, *n* = 83.

r, Spearman rank-order correlation coefficient.

NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable. ** Since the *p*-value was > 0.05 then we cannot reject H_0 in favour of H_1 at the 5% significance level; therefore growth is isometric.

Appendix 4.4 ***'Robust' least squares straight line equations and Spearman rank-order correlation coefficients for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on age (y)***

Dependent variable	**Linear regression**			
	n[a]	**Intercept ± S.E.**	**Slope ± S.E.**	***r* (*p*)**
Dorsal				
D1 Condylobasal length	51	5.15 ± 0.02	0.04 ± 0.00	0.89 (0.00)
D2 Gnathion to middle of occipital crest	49	4.97 ± 0.02	0.04 ± 0.00	0.92 (0.00)
D3 Gnathion to posterior end of nasals	49	4.04 ± 0.02	0.05 ± 0.00	0.87 (0.00)
D4 Greatest width of anterior nares	49	2.95 ± 0.03	0.04 ± 0.00	0.81 (0.00)
D5 Greatest length of nasals	47	3.30 ± 0.03	0.05 ± 0.00	0.76 (0.00)
D6 Breadth at preorbital processes	50	3.77 ± 0.02	0.05 ± 0.00	0.87 (0.00)
D7 Least interorbital constriction	49	3.09 ± 0.03	0.06 ± 0.00	0.89 (0.00)
D8 Breadth at supraorbital processes	45	3.60 ± 0.03	0.05 ± 0.00	0.85 (0.00)
D9 Breadth of brain case	51	4.38 ± 0.01	0.01 ± 0.00	0.31 (0.00)
Palatal				
P10 Palatal notch to incisors	50	4.24 ± 0.03	0.05 ± 0.00	0.84 (0.00)
P11 Length of upper postcanine row	50	3.78 ± 0.03	0.03 ± 0.00	0.59 (0.00)
P12 Greatest bicanine breadth	50	3.48 ± 0.02	0.05 ± 0.00	0.87 (0.00)
P13 Gnathion to posterior end of maxilla	50	4.36 ± 0.02	0.04 ± 0.00	0.83 (0.00)
P14 Breadth of zygomatic root of maxilla	52	2.45 ± 0.03	0.03 ± 0.00	0.57 (0.00)
P15 Breadth of palate at postcanine 1	43	2.57 ± 0.03	0.07 ± 0.00	0.89 (0.00)
P16 Breadth of palate at postcanine 3	43	2.89 ± 0.03	0.04 ± 0.00	0.77 (0.00)
P17 Breadth of palate at postcanine 5	49	3.05 ± 0.03	0.05 ± 0.00	0.74 (0.00)
P18 Gnathion to hind border of postglenoid process	46	4.79 ± 0.02	0.05 ± 0.00	0.92 (0.00)
P19 Bizygomatic breadth	51	4.50 ± 0.02	0.05 ± 0.00	0.89 (0.00)
P20 Basion to zygomatic root (anterior)	49	4.77 ± 0.02	0.04 ± 0.00	0.90 (0.00)
P21 Calvarial breadth	51	4.36 ± 0.02	0.04 ± 0.00	0.89 (0.00)
P22 Mastoid breadth	50	4.37 ± 0.02	0.06 ± 0.00	0.91 (0.00)
P23 Basion to bend of pterygoid	50	4.14 ± 0.02	0.02 ± 0.00	0.75 (0.00)
Lateral				
L24 Gnathion to foramen infraorbital	51	3.88 ± 0.03	0.05 ± 0.005	0.81 (0.00)
L25 Gnathion to hind border of preorbital process	50	3.92 ± 0.03	0.05 ± 0.00	0.87 (0.00)
L26 Height of skull at bottom of mastoid	39	4.17 ± 0.03	0.05 ± 0.005	0.79 (0.00)
L27 Height of sagittal crest	38	–	–	0.86 (0.00)
Mandibular				
M28 Length of mandible	50	4.70 ± 0.02	0.05 ± 0.00	0.91 (0.00)
M29 Length of mandibular tooth row	48	3.89 ± 0.02	0.04 ± 0.00	0.75 (0.00)
M30 Length of lower postcanine row	47	3.59 ± 0.02	0.03 ± 0.00	0.76 (0.00)
M31 Height of mandible at meatus	49	3.31 ± 0.04	0.08 ± 0.01	0.90 (0.00)
M32 Angularis to coronoideus	48	3.42 ± 0.03	0.07 ± 0.00	0.88 (0.00)
Log body length	44	4.53 ± 0.03	0.07 ± 0.00	0.87 (0.00)

[a] Number of skulls with skull variable and age recorded (only animals 1–10 y were included in analysis, i.e., *n* = 51).
r, Spearman rank-order correlation coefficient.
[Model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test for allometry not applicable].

Appendix 4.5 ***Spearman rank-order correlation coefficients for log skull variables according to region***

Frontal

	Var (D7)	**Var (D8)**
Var (D7)	1.00 (79)	0.93 (71)
Var (D8)	0.93 (71)	1.00 (75)

Nasal

	Var (D4)	**Var (D5)**
Var (D4)	1.00 (79)	0.81* (76)
Var (D5)	0.81* (79)	1.00 (78)

Neurocranium

	Var (D9)	**Var (L27)**
Var (D9)	1.00 (80)	0.25 (59)
Var (L27)	0.25 (59)	1.00 (60)

Zygomatic arch

	Var (P14)	**Var (P19)**
Var (P14)	1.00 (83)	0.71* (83)
Var (P19)	0.71* (83)	1.00 (83)

Basicranium

	Var (P21)	**Var (P22)**	**Var (P23)**
Var (P21)	1.00 (82)	0.97 (80)	0.88 (80)
Var (P22)	0.97 (80)	1.00 (82)	0.85 (81)
Var (P23)	0.88 (80)	0.85 (81)	1.00 (82)

Splanchnocranium

	Var (D3)	**Var (L24)**	**Var (L25)**
Var (D3)	1.00 (80)	0.94* (79)	0.96* (80)
Var (L24)	0.94* (79)	1.00 (82)	0.98* (81)
Var (L25)	0.96* (80)	0.98* (81)	1.00 (82)

Mandible

	Var (M28)	**Var (M29)**	**Var (M30)**	**Var (M31)**	**Var (M32)**
Var (M28)	1.00 (83)	0.83 (73)	0.79 (78)	0.88 (81)	0.88 (79)
Var (M29)	0.83 (73)	1.00 (74)	0.92 (69)	0.82 (72)	0.80 (71)
Var (M30)	0.79 (78)	0.92 (69)	1.00 (79)	0.78 (78)	0.80 (76)
Var (M31)	0.88 (81)	0.82 (72)	0.78 (78)	1.00 (82)	0.97 (80)
Var (M32)	0.88 (79)	0.80 (71)	0.80 (76)	0.97 (80)	1.00 (80)

Palate

	Var (P10)	**Var (P11)**	**Var (P12)**	**Var (P13)**	**Var (P15)**	**Var (P16)**	**Var (P17)**
Var (P10)	1.00 (82)	0.76* (81)	0.84* (81)	0.91* (81)	0.78* (72)	0.78* (72)	0.75* (79)
Var (P11)	0.76* (81)	1.00 (82)	0.76* (81)	0.79* (81)	0.76* (72)	0.76* (72)	0.64* (79)
Var (P12)	0.84* (81)	0.76* (81)	1.00 (82)	0.90* (81)	0.93* (73)	0.95* (73)	0.91* (80)
Var (P13)	0.91* (81)	0.79* (81)	0.90* (81)	1.00 (82)	0.84* (72)	0.84* (72)	0.83*(79)
Var (P15)	0.79* (72)	0.76* (72)	0.93* (73)	0.84* (72)	1.00 (73)	0.93* (72)	0.93* (72)
Var (P16)	0.78* (72)	0.76* (72)	0.95* (73)	0.84* (72)	0.93* (72)	1.00 (73)	0.95* (71)
Var (P17)	0.75* (79)	0.64* (79)	0.91* (80)	0.83* (79)	0.93* (72)	0.95* (71)	1.00 (80)

$p = 0.62$ for D4 and D5; $p = 0.00$ for all other variables.
* Significant at the 1% level (2-tailed).
Sample size in brackets.

CHAPTER 5

Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part three, baculum

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ABSTRACT

Morphology, relative size and growth of the baculum in 103 Cape fur seals, *Arctocephalus pusillus pusillus*, from the Eastern Cape coast of South Africa are described. Bacular measurements (n = 8 linear variables and mass) were examined in relation to standard body length (SBL), bacular length and chronological age (y) using linear regression. Animals ranged from < 1 mo to ≥ 12 y. Bacular shape was most similar to *Callorhinus* and *Zalophus*. For the range of ages represented in this study, the baculum continued to increase in size until at least 10 y, with growth slowing between 8–10 y, when social maturity (full reproductive capacity) is attained. Growth in bacular length, distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width, distal width and proximal shaft height peaked at 10 y. In the largest animals (age unknown), maximum bacular length was 139.3 mm and mass 12.5 g. Relative to SBL, bacular length increased rapidly in young animals, peaked at 9 y (6.9%), and then declined. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length. At 9 y, mean bacular length and mass was 117 mm and 7 g; growth rates in bacular length and mass were 311% and 7125% (relative to age zero), and 5% and 27% (between years); and bacular length averaged 6.9% of SBL. For all males ≥ 12 mo, most bacular variables grew at a faster rate than SBL and bacular length. Exceptions included proximal width which was isometric to SBL; distal width and distal shaft height which were isometric to bacular length; and proximal width which was negatively allometric relative to bacular length. Bacular length was found to be a 'rough indicator' of SBL and seal age group (pup, yearling, subadult, adult), but not of absolute age.

Key words: Pinnipeds, baculum, growth, allometry

INTRODUCTION

The mammalian baculum (os penis) is found in all carnivores, except the hyena (Ewer, 1973). This morphologically diverse bone has received considerable scientific attention in the field of mammalian systematics (McLaren, 1960; Sutton & Nadler, 1974; Kim *et al.*, 1975; Morejohn, 1975; Lee & Schmidly, 1977; Patterson & Thaeler, 1982; Patterson, 1983), and has been used as an index of age, puberty and social maturity for several species of mammals, including pinnipeds (Hamilton, 1939; Elder, 1951; Laws, 1956; Hewer, 1964; Bester, 1990). The function of the mammalian baculum remains controversial. It may lack specific function (Burt, 1939; Mayr, 1963) or may be adaptive in various interactions of males and females during copulation, with function differing considerably between species (Scheffer & Kenyon, 1963; Long & Frank, 1968; Ewer, 1973; Miller, 1974; Morejohn, 1975; Patterson & Thaeler, 1982; Eberhard, 1985, 1996; Dixson, 1995; Miller *et al.*, 1996, 1998, 1999).

Within the Otariidae, information on the morphology of the baculum is available for *Arctocephalus pusillus*, Afro-Australian fur seal; *Arctocephalus gazella*, Antarctic fur seal; *Callorhinus ursinus*, northern fur seal; *Eumetopias jubatus*, northern (Steller) sea lion; *Neophoca cinerea*, Australian sea lion; *Otaria byronia*, South American fur seal; *Phocarctos hookeri*, New Zealand (Hooker's) sea lion; and *Zalophus californianus*, California sea lion (Chaine, 1925; Hamilton, 1939; Rand, 1949, 1956; Scheffer, 1950; Mohr, 1963; Scheffer & Kenyon, 1963; Kim *et al.*, 1975; Morejohn, 1975; Laws & Sinha, 1993). Of these, the northern fur seal has been studied in most detail (Scheffer, 1950; Scheffer & Kenyon, 1963; Kim *et al.*, 1975; Morejohn, 1975).

Information on bacular growth based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), is only available for the northern fur seal (Scheffer, 1950); *Arctocephalus tropicalis*, subantarctic fur seal (Bester, 1990); and *Arctocephalus pusillus pusillus*, Cape fur seal (Oosthuizen & Miller, 2000). These studies indicate that: (i) the baculum increases in length and mass with increasing age; (ii) bacular growth may be fairly constant, as in the northern fur seal and subantarctic fur seal, or there may be an increase in the rate of growth at puberty, as in the Cape fur seal; (iii) there may be a sudden increase in the rate of bacular growth when individuals attain social maturity (full reproductive capacity); and (iv) there is a decline in the rate of bacular growth in socially mature animals.

Here we examine the bacula of 103 male Cape fur seals from the Eastern Cape coast of South Africa. Specific objectives were to: (i) describe the general morphology of the baculum; (ii) quantify growth of bacular measurements (n = 8 linear variables and mass) relative to standard body length (n = 89 animals), bacular length (n = 100 animals), and chronological age (n = 50 animals); (iii) determine if the baculum is a useful indicator of social maturity; and (iv) determine if bacular length is a useful indicator of age and/or standard body length. This study is the third in a series of papers initiated to develop baseline descriptions of Cape fur seal morphology and to examine growth patterns.

MATERIALS AND METHODS

Collection of specimens

Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). From this collection, bacula from 103 males were selected for examination (Appendix 5.1). Apart from specimens collected before May 1992 (n = 29), all specimens were collected by the first author. One animal (PEM2238) was collected NE of the study area, at Durban.

Preparation and measurement of bacula

Bacula were defleshed and macerated in water for 1–2 mo. Water was changed regularly. Bacula were then washed in mild detergent and air dried at room temperature. Dry specimens were weighed using an electronic balance and measurements (n = 8 linear variables) were taken using a vernier calliper (to 0.1 g and 0.1 mm) following Morejohn (1975) (Fig. 5.1). All bacular measurements, were recorded by the first author.

Age determination

Of the 103 animals in the study: (i) 40 were aged from counts of incremental lines observed in the dentine of upper canines as described in Stewardson *et al.*, (200X*a*). i.e., range 1–10 y; (ii) 10 were identified as adults > 12 y[1] (i.e., pulp cavity of the upper canine closed); and (iii) 52 were not aged.

For this study, the following age groups were used: pup (< 1 mo to 6 mo); yearling (7 mo to 1 y 6 mo); subadult (1 y 7 mo to 7 y 6 mo); and adult (≥ 7 y 7 mo) (Table 5.1). The following ages were not represented: 2 y and 3 y. Very old animals of known-age were not available for examination (estimated longevity *c.* 20 y).

Currently, examination of tooth structure is the most precise method of age determination in pinnipeds; however, counts are not without error. For information of the reliability of this method see Oosthuizen (1997).

Statistical analysis

Bacular measurement error

Duplicate measurements of bacular length were taken from 50 randomly selected bacula to assess measurement error. The Wilcoxon sign-rank test was

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[1] In Cape fur seals, animals > 13 y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes which terminates tooth growth, hence the age group '> 12 y'.

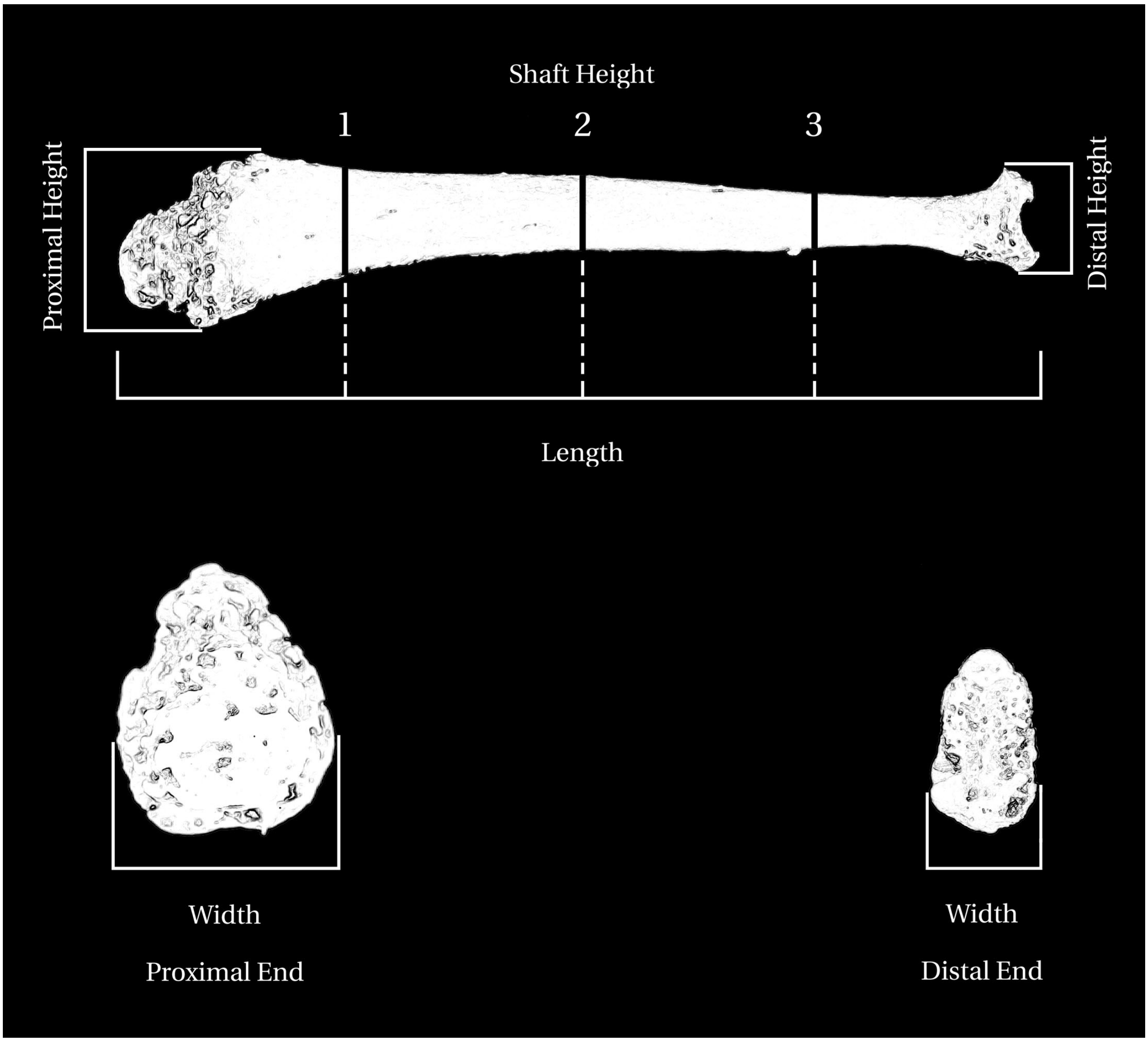


Fig. 5.1 Diagram of a Cape fur seal baculum showing how individual measurements were taken.
a. bacular length; b. proximal height; c. proximal width; d. distal height; e. distal width; f (1). proximal shaft height; f (2). middle shaft height; f (3). distal shaft height; g. bacular mass (not shown). Specimen provided by P. Shaughnessy.

used on the differences to test H_0 : median = 0, versus H_1 : median ≠ 0.

Bacular length expressed in relation to standard body length

Growth in bacular length, relative to standard body length (SBL), was calculated as follows, using paired samples only:

$$\text{bacular length (mm)/SBL (mm)} \times 100\%$$

As the approximate variance of the ratio estimate is difficult to calculate, percentages must be interpreted with caution (Cochran, 1977, p. 153).

Bacular growth relative to age zero, RGR $\bar{y}_0$

Percent change in bacular measurement at age *t*, relative to value at age zero, was calculated as follows:

$$[(\bar{y}_t - \bar{y}_0)/\bar{y}_0] \times 100\%$$

where $\bar{y}_0$ = bacular measurement from pups < 1 mo of age (age zero), and $\bar{y}_t$ = bacular measurement for age *t* (age class in y).

Bacular growth relative to the previous year, RGR $\bar{y}_{t-1}$

The percent change in value at age *t*, relative to the value at age *t*–1, was calculated as follows:

$$[(\bar{y}_t - \bar{y}_{t-1})/\bar{y}_{t-1}] \times 100\%$$

where $\bar{y}_t$ = as above, and $\bar{y}_{t-1}$ = bacular measurement for age *t*–1 (between years). RGRs were calculated for animals 7–10 y.

Bacular length as an indicator of SBL and age

The degree of linear relationship between log bacular length, log SBL and age (y) was calculated using the

Spearman rank-order correlation coefficient. Linear discriminant function analysis (Mahalanobis squared distance) was used to predict the likelihood that an individual seal will belong to a particular age group (pup, yearling, subadult, adult) using one independent variable, bacular length (see Stewardson *et al.*, 200X*a* for further details).

Bivariate allometric regression

The relationship between value of bacular measurement and: (i) SBL, (ii) bacular length, and (iii) age (y), was investigated using the logarithmic (base e) transformation of the allometric equation, y = ax^b, which may equivalently be written as log y = log a + b log x. 'Robust' regression (Huber M-Regression) was used to fit straight lines to the transformed data. The degree of linear relationship between the transformed variables was calculated using the Spearman rank-order correlation coefficient, r (Gibbons & Chakraborti, 1992). Testing of model assumptions, and hypotheses about the slope of the line, followed methods described by Stewardson *et al.*, 200X*a*.

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23); Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

RESULTS

Bacular measurement error

Of the 50 bacula that were measured twice, measurements were reproducible at the 5% significance level (p-value = 0.03).

Table 5.1 *The age distribution of Cape fur seals*

Age group	Age[a] (y)	Frequency	Percentage
Pup[b]	0	3	6.0
Yearling	1	5	10.0
Subadult	2	0	0.0
	3	0	0.0
	4	1	2.0
	5	3	6.0
	6	2	4.0
	7	11	22.0
Adult	8	8	16.0
	9	4	8.0
	10	3	6.0
	> 12	10	20.0
Total		**50**	**100**

[a] Age inferred from counts of incremental lines observed in the dentine of upper canine (n = 40). An additional 10 males were > 12 y, i.e., pulp cavity closed.

[b] < one month of age.

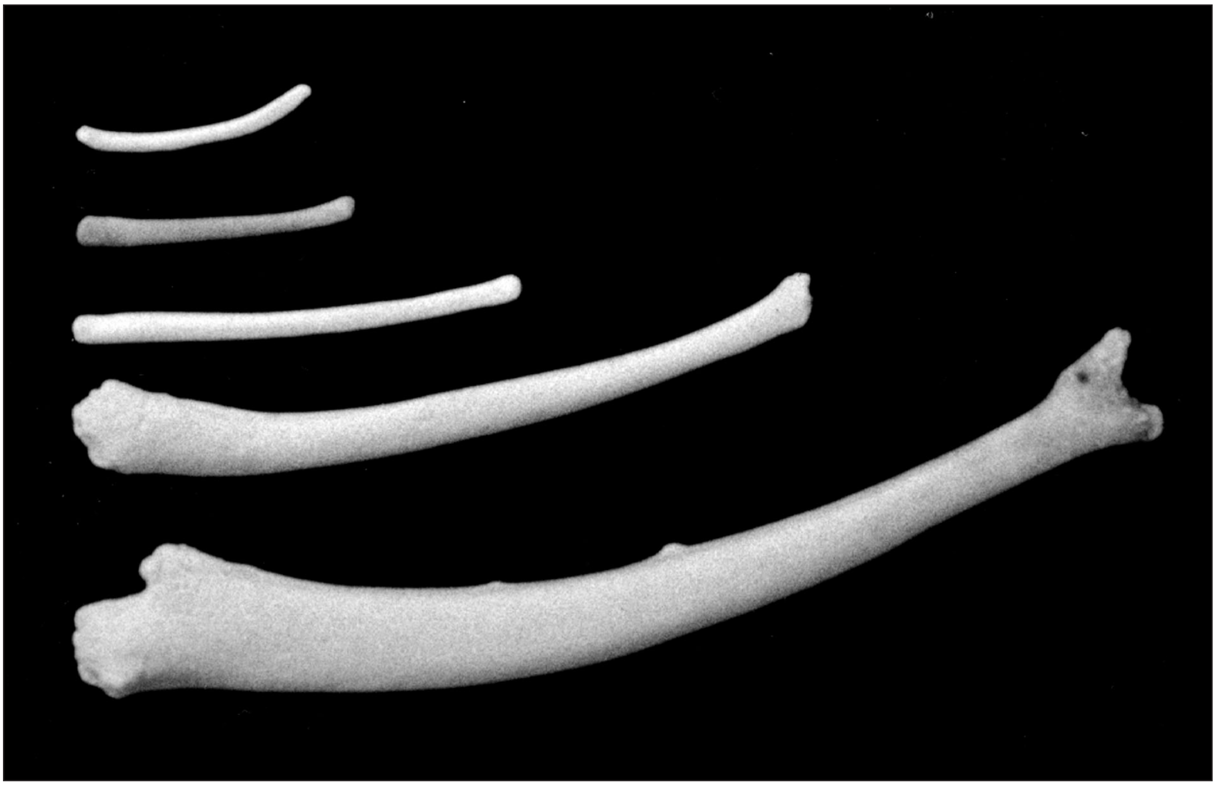


Fig. 5.2 Size and shape of the Cape fur seal baculum in relation to age group.
1. pup (PEM2020, 26.6 mm); 2. pup (PEM2024, 31.6 mm); 3. yearling (PEM2191, 50.7 mm); 4. subadult, 7-y-old (PEM2053, 93.3 mm); 5. adult, 10-y-old (PEM2087, 123.3 mm).

Table 5.2 *Summary statistics for bacular variables (1–9), according to age (y) and age group.* Data presented as mean measurement ± S.E., followed by coefficient of variation in round brackets, and bacular variable expressed as a percentage of bacular length. Maximum value of each variable (males of unknown-age) is also presented. All measurements are in mm, apart from bacular mass (g).

Age group	Age (y)	*n*[a]	Var 1	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	28.5 ± 1.6	2.6 ± 0.5	3.5 ± 0.3	2.2 ± 0.3	1.7 ± 0.2	2.4 ± 0.2	2.2 ± 0.2	1.9 ± 0.1	0.1 ± 0.0
			(9.6) –	(31.5) 9.0%	(12.5) 12.3%	(24.7) 7.8%	(18.3) 5.9%	(13.6) 8.3%	(15.7) 7.7%	(7.9) 6.8%	(0) 0.4%
Yearling	1	5	47.8 ± 1.7	3.5 ± 0.1	4.2 ± 0.1	2.9 ± 0.2	1.7 ± 0.04	3.0 ± 0.1	2.5 ± 0.1	2.2 ± 0.2	0.3 ± 0.03
			(8.0) –	(7.7) 7.3%	(6.6) 8.8%	(15.8) 6.1%	(5.9) 3.6%	(5.0) 6.2%	(12.2) 5.2%	(18.2) 4.6%	(23.6) 0.6%
Subadult	4	1*	86.6	5.3	6.6	7.3	2.8	5.9	5.5	4.4	2.4
	5	3	97.1 ± 4.6	9.4 ± 2.5	7.7 ± 0.9	9.4 ± 0.6	4.2 ± 0.8	7.0 ± 0.6	5.8 ± 0.2	5.0 ± 0.2	3.4 ± 0.4
			(8.2) –	(45.3) 9.7%	(20.9) 7.9%	(10.5) 9.7%	(31.0) 4.3%	(13.6) 7.2%	(4.6) 6.0%	(8.4) 5.1%	(21.2) 3.5%
	6	2	99.5 ± 2.8	8.2 ± 0.1	6.7 ± 1.5	10.9 ± 0.1	3.9 ± 0.6	7.1 ± 0.9	5.4 ± 0.2	4.5 ± 0.1	3.1 ± 0.1
			(3.9) –	(0.9) 8.2%	(31.7) 6.7%	(0.7) 10.9%	(20.2) 3.9%	(17.9) 7.1%	(5.2) 5.4%	(3.1) 4.5%	(2.3) 3.1%
	7	11	101.4 ± 2.7	9.8 ± 1.0	7.6 ± 0.4	10.7 ± 0.6	4.0 ± 0.2	7.2 ± 0.3	6.3 ± 0.3	5.3 ± 0.2	4.1 ± 0.4
			(9.0) –	(33.4) 9.7%	(16.3) 7.5%	(17.8) 10.5%	(17.5) 4.0%	(14.8) 7.1%	(13.3) 6.2%	(14.3) 5.3%	(34.0) 4.0%
	4–7	**17**	**99.5 ± 2.1**	**9.3 ± 0.8**	**7.5 ± 0.3**	**10.3 ± 0.4**	**4.0 ± 0.2**	**7.1 ± 0.2**	**6.1 ± 0.2**	**5.1 ± 0.2**	**3.7 ± 0.3**
			(8.7) –	(34.6) 9.3%	(17.5) 7.5%	(17.5) 10.3%	(20.5) 4.0%	(14.4) 7.1%	(12.5) 6.1%	(13.9) 5.1%	(33.1) 3.7
Adult	8	8	111.4 ± 3.1	11.3 ± 0.8	9.4 ± 0.6	12.2 ± 0.5	4.3 ± 0.1	8.0 ± 0.3	6.9 ± 0.2	5.6 ± 0.2	5.7 ± 0.5
			(7.8) –	(19.0) 10.8%	(18.5) 8.4%	(12.3) 11.0%	(9.5) 3.9%	(11.1) 7.2%	(8.7) 6.1%	(8.4) 5.0%	(23.9) 5.1%
	9	4	116.9 ± 2.7	10.4 ± 1.8	10.8 ± 1.6	12.4 ± 0.9	4.9 ± 0.7	8.1 ± 0.5	7.6 ± 0.3	6.3 ± 0.2	7.2 ± 0.7
			(4.6) –	(35.5) 8.9%	(29.3) 9.2%	(14.5) 10.6%	(29.2) 4.2%	(12.8) 7.0%	(7.9) 6.5%	(7.8) 5.4%	(18.4) 6.2%
	10	3	117.8 ± 2.9	14.0 ± 0.8	13.5 ± 1.9	13.2 ± 0.5	6.1 ± 0.4	10.6 ± 0.3	8.1 ± 0.4	6.5 ± 0.2	7.6 ± 0.6
			(4.3) –	(9.7) 11.9%	(24.5) 11.4%	(6.2) 11.2%	(12.5) 5.2%	(4.8) 9.0%	(8.1) 6.9%	(4.7) 5.5%	(14.1) 6.5%
	8–10	**15**	**114.2 ± 2.0**	**11.6 ± 0.7**	**10.6 ± 0.7**	**12.5 ± 0.4**	**4.8 ± 0.3**	**8.6 ± 0.3**	**7.3 ± 0.2**	**6.0 ± 0.1**	**6.5 ± 0.4**
			(6.6) –	(23.1) 10.2%	(26.4) 9.3%	(11.5) 10.9%	(22.0) 4.2%	(15.4) 7.5%	(10.6) 6.4%	(9.6) 5.2%	(23.2) 6.7%
	> 12	10	113.1 ± 3.8	11.4 ± 0.8	10.1 ± 0.7	13.3 ± 0.7	4.9 ± 0.5	10.0 ± 0.5 [8]	8.6 ± 0.6	6.6 ± 0.3	8.3 ± 0.9
			(10.7) –	(22.6) 10.1%	(20.9) 8.9%	(17.3) 11.7%	(28.4) 4.5%	(17.2) 8.8%	(23.6) 7.6%	(12.5) 5.8%	(34.2) 7.3%
Total		**50**	**50**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**
Mean for males ≥ 200 cm[b] [max. value in brackets]			127.7 ± 2.8 [139.3]	13.1 ± 0.3 [14.0]	9.9 ± 1.0 [13.7]	14.4 ± 0.4 [15.7]	5.0 ± 0.3 [5.8]	10.5 ± 0.5 [12.2]	9.2 ± 0.3 [10.2]	7.1 ± 0.3 [8.1]	10.9 ± 0.5 [12.5]

Variables: 1. bacular length; 2. proximal height; 3. proximal width; 4. distal height; 5. distal width; 6. proximal shaft height; 7. middle shaft height; 8. distal shaft height; 9. bacular mass.

[a] Number of bacula for canine aged animals. Sample size given in square brackets where this does not equal total sample size.

[b] Mean value of variable ± S.E. for the 7 largest males (≥ 200 cm) of unknown-age; maximum value in brackets.

* S.E. of one measurement can not be measured.

Table 5.3 *Growth in mean bacular length relative to mean standard body length*

Age group	Age (y)	n[a]	Mean bacular length[b] (mm)	Mean SBL[c] (cm)	Bacular length rel. to SBL[d]
Pup	< 1	3	28.5 ± 1.6	69.0 ± 2.5	4.1%
Yearling	1	5	47.8 ± 1.7	90.6 ± 2.7	5.3 %
Subadult	4	1*	86.6	137.0	–
	5	3	– [0]	– [0]	–
	6	2	102.2 [1*]	145.0 [1*]	–
	7	11	106.5 ± 3.0 [6]	159.8 ± 4.5 [6]	6.7% [6]
	4–7	**17**	**103.5 ± 3.3 [8]**	**155.1 ± 4.6 [8]**	**–**
Adult	8	8	110.0 ± 3.2 [7]	167.1 ± 7.1 [7]	6.6% [7]
	9	4	117.3 ± 3.8 [3]	171.0 ± 3.2 [3]	6.9% [3]
	10	3	117.8 ± 2.9	187.0 ± 1.7	6.3%
	8–10	**15**	**113.5 ± 2.2 [13]**	**172.6 ± 4.4 [13]**	**6.6%[13]**
	> 12	10	113.2 ± 4.3 [9]	185.9 ± 7.7 [9]	6.1% [9]
Total		**50**	**38**	**38**	**38**

[a] Number of canine aged animals with both bacular length and SBL recorded. Of the 50 canine aged animals, SBL was not recorded for 12 animals, i.e. n = 38. Sample size is given in square brackets where this does not equal total sample size.

[b] Bacular length (mean ± S.E.).

[c] Standard body length (mean ± S.E.). SBL is defined as the length from the nose to the tail in a straight line with the animal on its back.

[d] Bacular length (mm)/SBL (mm) × 100%.

* S.E. of one measurement can not be measured.

Bacular morphology

Bacular length and mass ranged from 26.6 to 139.3 mm and 0.1 to 12.5 g, respectively (Table 5.2).

The youngest animals in the sample were < 1 mo of age. In these individuals, the baculum was short, thin and rod-like, with no obvious distinction between the proximal and distal ends (Fig. 5.2). The shaft was slightly curved anteriorly (variable).

In yearlings, the baculum increased substantially in length and mass (Table 5.3). The distal end was slightly rounded but, there was no sign of bifurcation (Fig. 5.2).

In subadults, most bacula curved upwards at the distal end (i.e., superiorly). At the distal end of the baculum, there were two narrow projections (knobs): a well-developed ventral knob and a less prominent dorsal knob (Fig. 5.2). In older subadults, the ventral knob extended upwards and outwards forming a double knob (variable). The proximal end of the bacula was bulbous in all animals ≥ 4 y.

In adults 8 and 9 y of age the baculum was well-developed, with pronounced thickening of the proximal end (Fig. 5.2). At the bifurcated distal end, the ventral knob usually extended further than the dorsal knob. In older males, the baculum was more robust, but not necessarily longer. Small osseous growths were commonly found on the proximal end of the baculum (n = 18 subadult and adult bacula) creating a rough surface where the fibrous tissue of the *corpus cavernosum penis* attached. In some older specimens (n = 16 bacula), small knob-like growths (usually 1 or 2) were observed along the edge of the urethral groove, at the proximal ventral surface of the baculum.

Bacular length expressed in relation to SBL

Relative to SBL, bacular length increased rapidly in young animals, peaked at 9 y (6.9%), and then declined in animals ≥ 10 y, i.e., 6.3% (10 y); 6.1% (> 12 y) (Table 5.3). Relative growth patterns for subadults < 7 y could not be established because SBL was not available for all specimens (SBLs for 14 animals were not recorded, i.e., curve body lengths were recorded for seals measured in rough conditions at sea).

Bacular growth relative to age zero, RGR $\bar{y}_0$

Percent change in value of bacular measurement at age t, relative to value at age zero, is presented in Table 5.4.

In yearlings, bacular mass was the most rapidly growing variable, followed by bacular length, proximal height, distal height, proximal shaft height, proximal width and distal shaft height/middle shaft height. Distal width showed little sign of growth.

Growth of bacular variables continued to increase until at least 10 y, with bacular mass, middle shaft height and distal shaft height expressing continued growth in animals > 12 y. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length (Table 5.4).

Bacular growth relative to the previous year, RGR $\bar{y}_{t-1}$

Percent change in value of bacular measurement at age t, relative to value at age t–1, for animals 7–10 y, is presented in Table 5.4. Percent increment in bacular length, distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width distal width and proximal shaft height peaked at 10 y.

Table 5.4 *Growth in bacular variables (1–9) relative to the mean value of bacular measurement: (i) at age zero, RGR*$_{\bar{y}_0}$ *and (ii) from the previous year, RGR*$_{\bar{y}_{t-1}}$. **Growth in SBL is also given. All measurements are in mm, apart from SBL (cm) and bacular mass (g).**

Age group	Age (y)	n[a]	SBL[b]	Var 1	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	–	–	–	–	–	–	–	–	–	–
Yearling	1	5	31	68	36	21	31	2	26	13	14	200
Subadult	4	1	99	204	106	89	227	68	149	150	128	2300
	5	3	– [0]	241	266	120	322	152	196	164	157	3300
	6	2	110 [1]	249	218	91	386	131	200	145	133	2950
	7	11	132; – [6]	256; 2.0	282; 20.4	118; 13.7	379; -1.5	143; 5.1	206; 2.0	186; 16.5	176; 18.8	3964; 33.2
Adult	8	8	142; 4.6 [7]	391; 9.9	341; 15.3	169; 23.4	448; 14.5	158; 6.3	239; 10.8	211; 8.9	191; 5.2	5600; 40.3
	9	4	148; 2.3 [3]	311; 4.9	304; -8.3	209; 14.9	453; 0.9	193; 13.4	243; 1.2	245; 10.9	225; 11.6	7125; 26.8
	10	3	171; 9.4	313; 0.8	447; 35.3	285; 24.7	491; 6.9	268; 25.8	346; 30.1	268; 6.6	234; 3.1	7533; 5.7
	> 12	10	169 [9]	297	343	189	495	196 [8]	320	290	241	8150
Total		**50**	**38**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**	**50**

Variables: 1. bacular length; 2. proximal height; 3. proximal width; 4. distal height; 5. distal width; 6. proximal shaft height; 7. middle shaft height; 8. distal shaft height; 9. bacular mass.

[a] Number of bacula for canine aged animals.

[b] SBLs for 12 of these animals were not recorded.

Values for growth relative to age zero are presented on the left hand side of the relevant columns, i.e., $[(\bar{y}_t - \bar{y}_0)/\bar{y}_0] \times 100\%$. Values for growth relative to the previous year are presented on the right hand side of the relevant columns, for animals 7–10 y of age, i.e., $[(\bar{y}_t - \bar{y}_{t-1})/\bar{y}_{t-1}] \times 100\%$.

Sample size given in square brackets where this does not equal total sample size.

Bacular length as an indicator of age

For animals 1–10 y, bacular length was highly, positively correlated with age (y) ($r = 0.83$, $n = 37$; Fig. 5.5a). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate (the residuals were not scattered randomly about zero, see Weisberg, 1985, p. 23). Thus, bacular length could not be used as a reliable indicator of absolute age.

For the range of ages available in this study, the coefficient of variation in bacular length for young males 1–5 y (36.8%) was considerably higher than in older males (8–10 y, 6.6%; > 12 y, 10.7%) Table 5.2.

Although bacular length was not a good indicator of absolute age, it was a 'rough indicator' of age group. When bacular length is known, the following linear discriminant functions can be used to categorise each observation into one of four age groups (pups, yearlings, subadult, adults):

$$y_0 = -5.50 + 0.39x$$
$$y_1 = -15.53 + 0.65x$$
$$y_2 = -67.25 + 1.35x$$
$$y_3 = -87.77 + 1.54x$$

where x = bacular length (mm); subscript 0 = pup; subscript 1 = yearling; subscript 2 = subadult; and subscript 3 = adult. The seal is classified into the age group associated with the linear discriminant function which results in the minimum value. Of the 50 observations in this study, 86% were correctly classified using this method (Table 5.5).

Bacular length as an indicator of SBL

Bacular length was highly, positively correlated with SBL ($r = 0.88$, $n = 86$; Fig. 5.3a). When bacular length is known, the following equation (linear least squares fit; untransformed data) can be used as a 'rough indicator' of SBL:

$$y = 36.42 + 1.24x$$

which may equivalently be written as SBL = $e^{36.42} \times$ bacular length$^{1.24}$, where the S.E. of the intercept is 4.98 and the S.E. of the slope is 0.05 ($n = 86$).

Bivariate allometric regression

With one exception, bacular variables were significantly, positively correlated with each other, $r \geq 0.7$ (Table 5.6). Distal width with proximal width ($r = 0.67$) was the only exception.

Value of bacular measurement on SBL

Of the 103 seals in the study, 86 were used in regression analysis for log of baculum measurement on log SBL, i.e., all pups ($n = 3$) were excluded from regression analysis, and SBLs for 14 animals were not recorded.

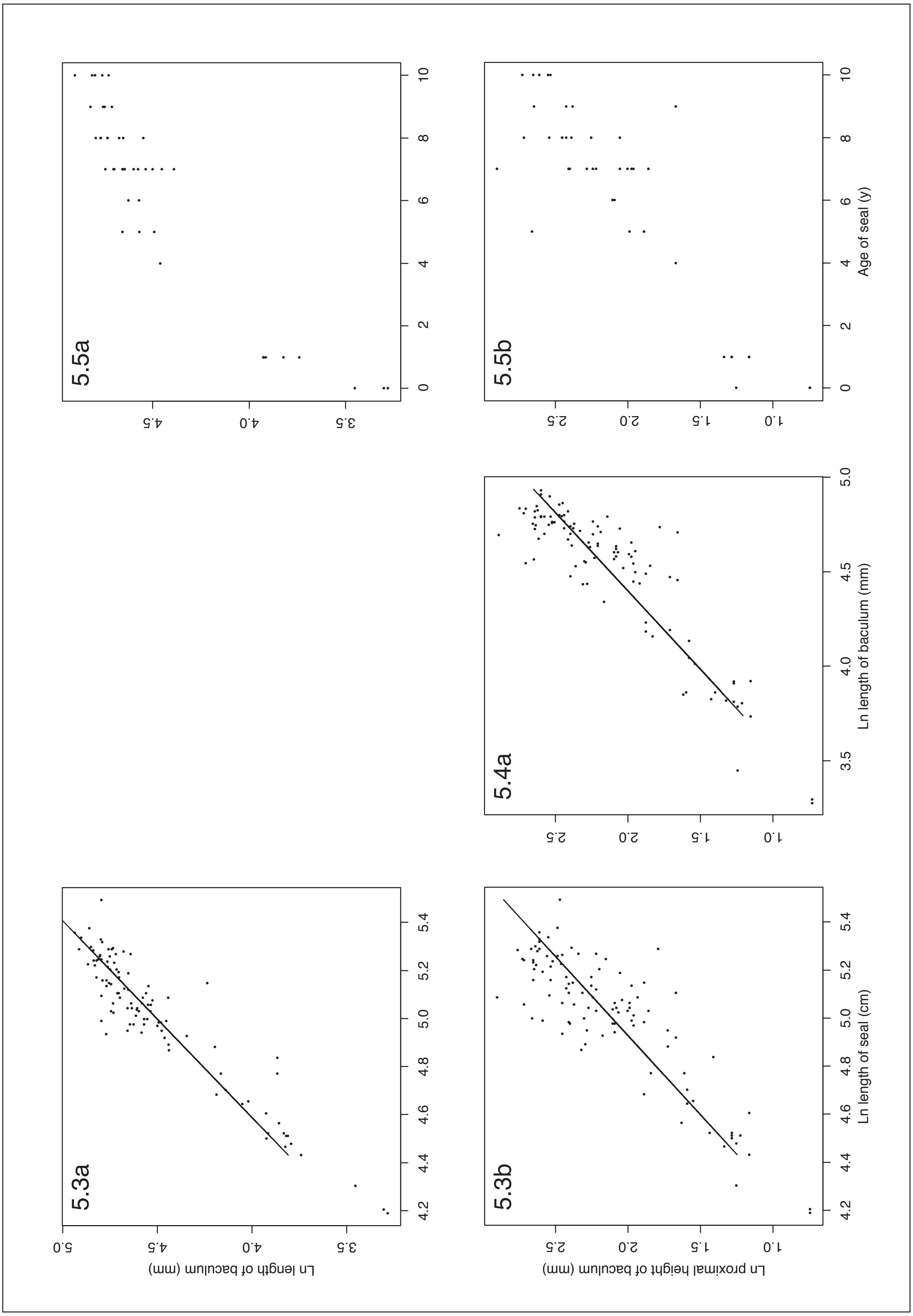


Fig. 5.3a, 5.3b Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4a Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5a, 5.5b Bivariate plot of log baculum measurement (mm) on age of seal (y).

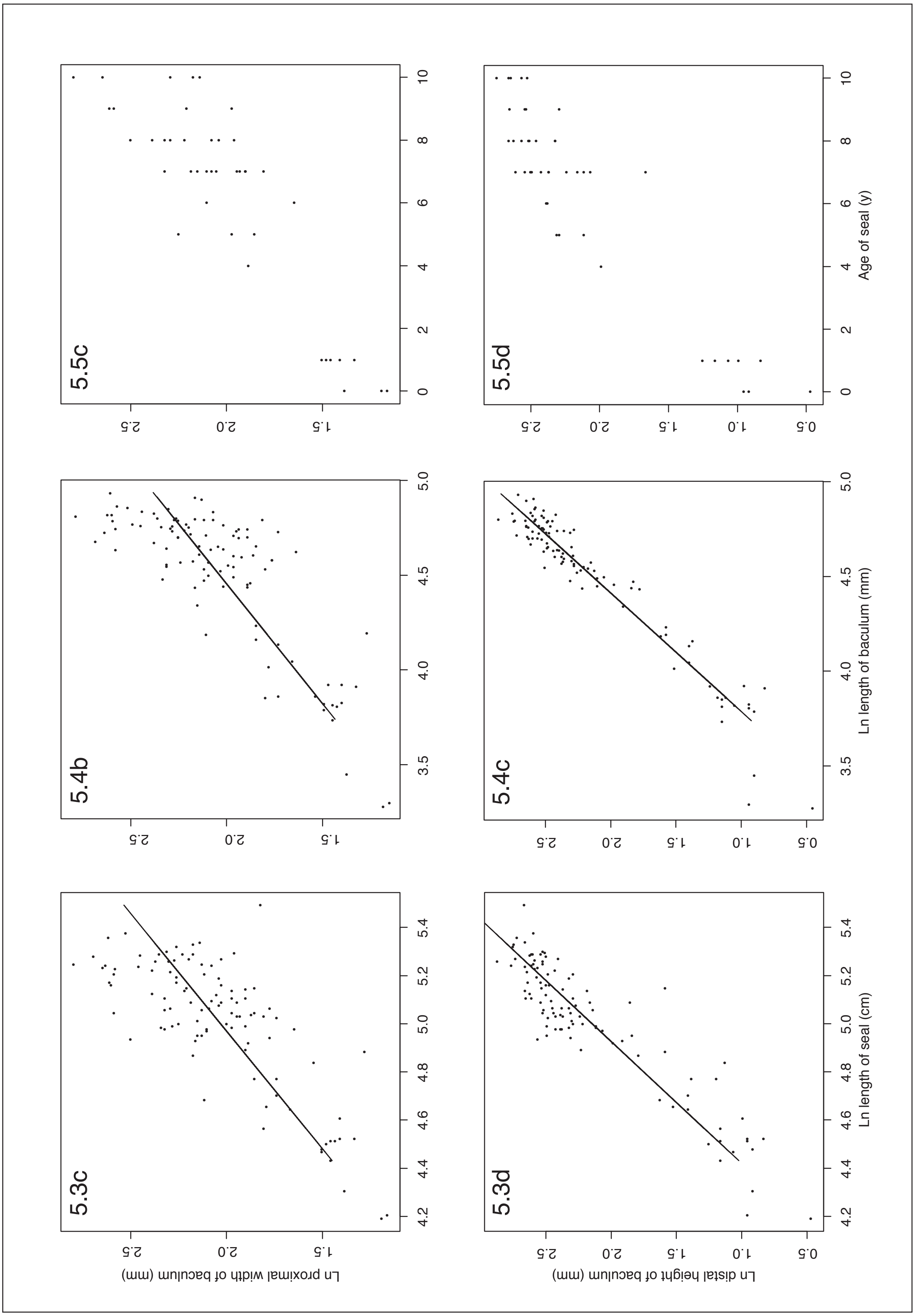


Fig. 5.3c, 5.3d Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4b, 5.4c Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5c, 5.5d Bivariate plot of log baculum measurement (mm) on age of seal (y).

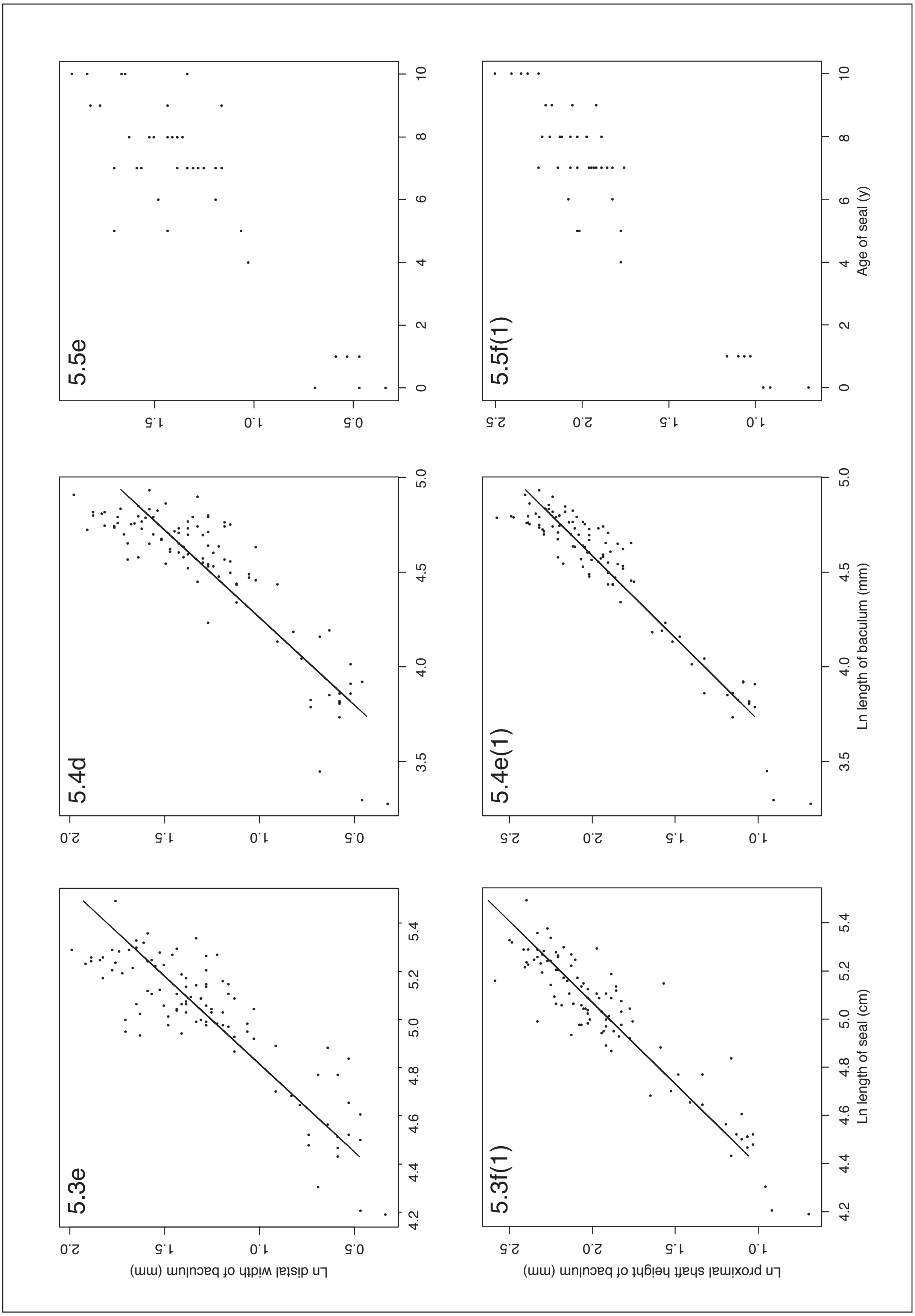


Fig. 5.3e, 5.3f(1) Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4d, 5.4e(1) Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5e, 5.5f(1) Bivariate plot of log baculum measurement (mm) on age of seal (y).

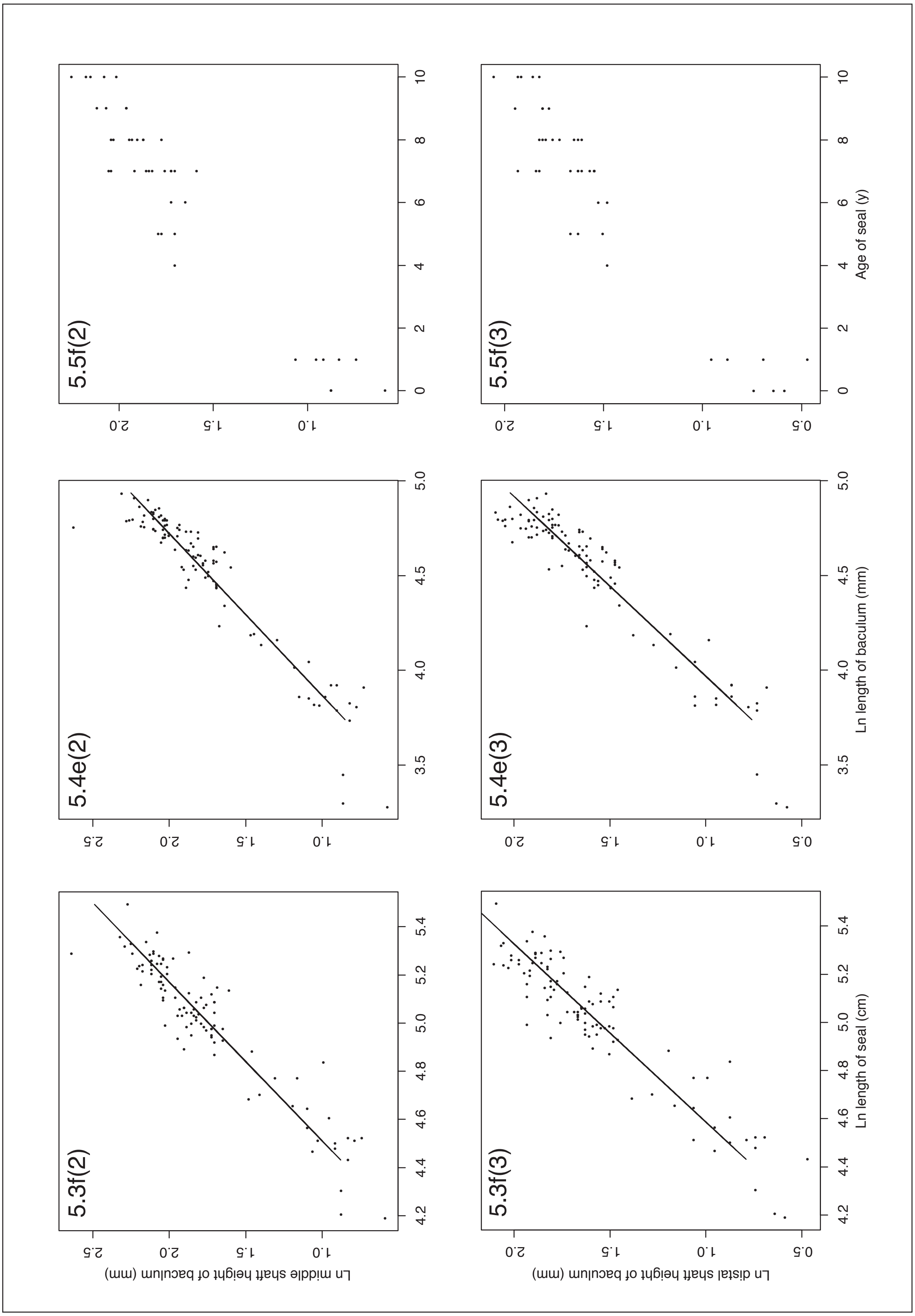
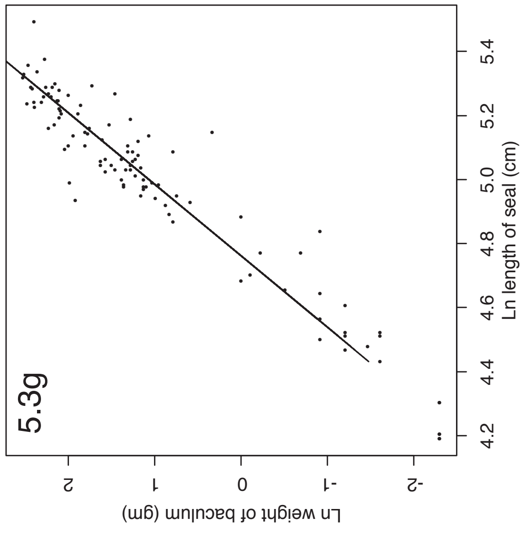
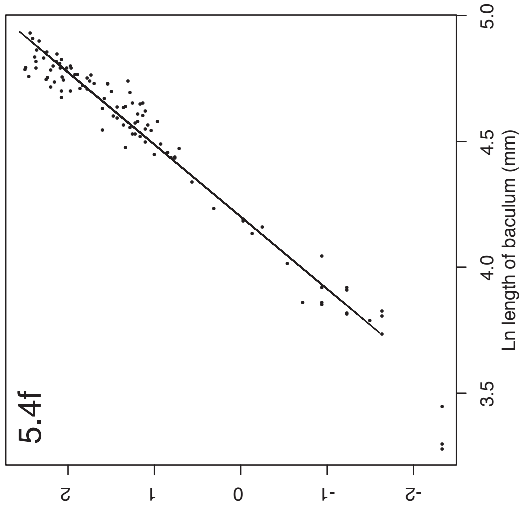
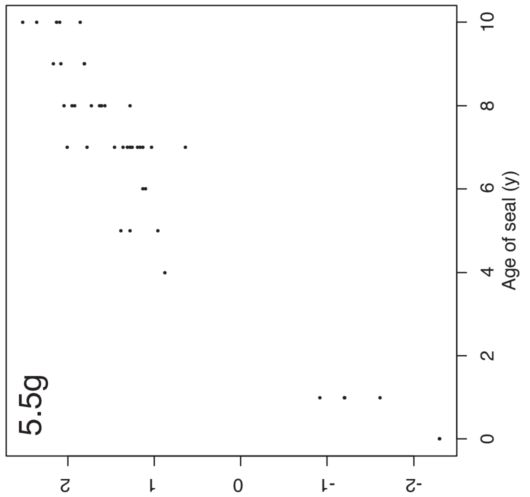


Fig. 5.3f(2), 5.3f(3) Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4e(2), 5.4e(3) Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5f(2), 5.5f(3) Bivariate plot of log baculum measurement (mm) on age of seal (y).







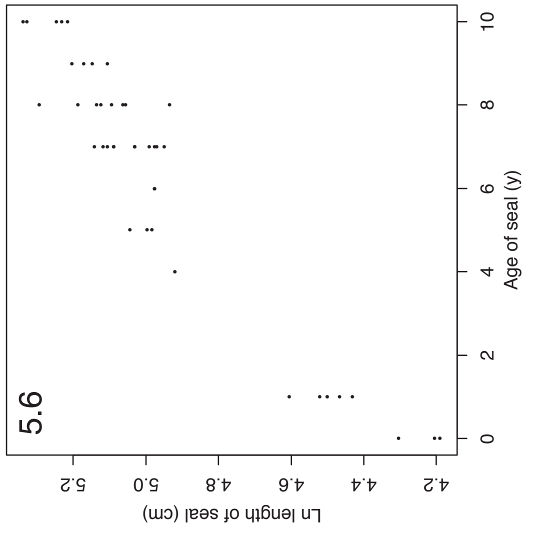


Fig. 5.3g Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4f Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5g Bivariate plot of log baculum measurement (mm) on age of seal (y).
Fig 5.6 Bivariate plot of log length of seal (cm) on age of seal (y).

There was little difference between the ordinary least square straight lines fitted to the data, and the 'robust' least squares straight lines fitted to the data. The 'robust' straight line equations for regressing log of baculum measurement on log of seal length are given in Table 5.7.

All bacular variables were highly, positively correlated with SBL, $r \geq 0.7$ (Fig. 5.3a–g; Table 5.7). Proximal width ($r = 0.68$) was the only exception.

Relative to SBL, growth in distal height, distal width, proximal shaft height, distal shaft height and bacular mass was positively allometric; and proximal width was isometric (Table 5.7). Regression slopes for bacular length, proximal height and middle shaft height scaled with positive slope (Table 5.7).

Value of bacular measurement on bacular length

Of the 103 seals in the study, 100 were used in regression analysis for log of baculum measurement on bacular length, i.e., all pups (n = 3) were excluded from regression analysis.

All bacular variables were highly, positively correlated with bacular length, $r \geq 0.7$ (Fig. 5.4a–f; Table 5.8). Relative to bacular length, growth in distal height, proximal shaft height and proximal height was positively allometric relative to bacular length; distal width and distal shaft height was isometric; and proximal width was negatively allometric (Table 5.8). Regression slopes for middle shaft height and bacular mass scaled with positive slope (Table 5.8). The slope for bacular mass was considerably steeper than for other variables.

Value of bacular measurement on age

Of the 40 seals aged from upper canines, 37 were used in regression analysis for log of baculum measurement versus age, i.e., all pups (n = 3) were excluded from regression analysis.

Overall, the plots of log bacular measurements versus log SBL were better described by linear relationships than the plots of log bacular measurements versus age, even though the assoc-iated correlation coefficients were moderately to strongly positive (see Griffiths *et al.*, 1998, p. 126) (Fig. 5.5a–g; Table 5.9). Proximal height was the only variable that roughly resembled a straight line (Fig. 5.5b). All variables scaled with negative slope relative to age.

Table 5.5 *Discriminant analysis for seal age group (pup, yearling, subadult, adult) inferred from bacular length*

Known age group		**Classification into age group**			
		0	**1**	**2**	**3**
	***n*[a]**	Pup (< 1 mo)	Yearling (7 mo to 1 y 6 mo)	Subadult (1 y 7 mo to 7 y 6 mo)	Adult[b] (≥ 7 y 7 mo)
0	**3**	3 (100%)	0	0	0
1	**5**	0	5 (100%)	0	0
2	**17**	0	0	14 (82%)	4
3	**25**	0	0	3	21 (84%)
Total	**50**	**3**	**5**	**17**	**25**

[a] Number of animals aged from counts of incremental lines observed in the dentine of upper canines, n = 50. Percentage of animals correctly classified into age group is given in brackets.
[b] Included animals > 12 y.

Table 5.6 *Spearman rank-order correlation coefficients for log bacular variables*

	Var 1	**Var 2**	**Var 3**	**Var 4**	**Var 5**	**Var 6**	**Var 7**	**Var 8**	**Var 9**
Var 1	1.00	0.82	0.71	0.90	0.80	0.88	0.92	0.90	0.95
Var 2	0.82	1.00	0.80	0.76	0.75	0.85	0.84	0.80	0.85
Var 3	0.71	0.80	1.00	0.69	*0.67*	0.76	0.75	0.70	0.77
Var 4	0.90	0.76	0.69	1.00	0.80	0.86	0.89	0.88	0.92
Var 5	0.80	0.75	*0.67*	0.80	1.00	0.79	0.80	0.80	0.83
Var 6	0.88	0.85	0.76	0.86	0.79	1.00	0.94	0.89	0.94
Var 7	0.92	0.84	0.75	0.89	0.79	0.94	1.00	0.96	0.97
Var 8	0.90	0.80	0.70	0.88	0.80	0.89	0.96	1.00	0.95
Var 9	0.95	0.85	0.77	0.92	0.83	0.94	0.97	0.95	1.00
Total	**103**	**103**	**103**	**103**	**101[a]**	**103**	**103**	**103**	**103**

Variables: 1. bacular length; 2. proximal height; 3. proximal width; 4. distal height; 5. distal width; 6. proximal shaft height; 7. middle shaft height; 8. distal shaft height; 9. bacular mass.
[a] Two distal width measurements were not recorded, i.e., PEM2049 and PEM2134.
All correlations are significant at the 1% level (2-tailed), i.e., $P = 0.00$.

Table 5.7 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients and allometry for log bacular measurement (mm) on log seal body length (cm)***

Dependent variable		**Linear regression**			**Allometry**		
	n[a]	**Intercept ± S.E.**	**Slope ± S.E.**	***r* (*p*-values)**	**Alternative hypothesis**	***d.f.***	***p*-value**
1. Length of baculum	86	-1.67 ± 0.22	1.23 ± 0.04	0.88 (0.00)	NA	NA	NA
2. Proximal height	86	-5.58 ± 0.45	1.54 ± 0.09	0.78 (0.00)	NA	NA	NA
3. Proximal width	86	-3.12 ± 0.48	1.03 ± 0.09	0.68 (0.00)	$H_1 : \hat{\beta} \neq 1$	84	0.78*
4. Distal height	86	-7.88 ± 0.46	2.00 ± 0.09	0.84 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
5. Distal width	84[b]	-5.64 ± 0.04	1.38 ± 0.09	0.80 (0.00)	$H_1 : \hat{\beta} > 1$	82[b]	0.00
6. Proximal shaft height	86	-5.59 ± 0.29	1.50 ± 0.06	0.87 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
7. Middle shaft height	86	-5.92 ± 0.28	1.53 ± 0.06	0.90 (0.00)	NA	NA	NA
8. Distal shaft height	86	-5.24 ± 0.29	1.36 ± 0.06	0.87 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
9. Mass of baculum	86	-21.51 ± 0.68	4.51 ± 0.13	0.91 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
Total	**86**						

[a] Number of bacula for canine aged animals and animals of unknown-age (the 3 pups were excluded from analysis, and SBLs from 14 males were not recorded, i.e., *n* = 86 bacula).

[b] Two distal width measurements were not recorded for PEM2049 and PEM2134.
r, Spearman rank-order correlation coefficient.
All correlations are significant at the 1% level (2-tailed).
NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.
* Since the p-value was > 0.05, we cannot reject H_0 in favour of H_1 at the 5% significance level; therefore growth is isometric.

Table 5.8 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients and allometry for log bacular measurement (mm) on log bacular length (mm)***

Dependent variable		**Linear regression**			**Allometry**		
	n[a]	**Intercept ± S.E.**	**Slope ± S.E.**	***r* (*p*-values)**	**Alternative hypothesis**	***d.f.***	***p*-value**
2. Proximal height	100	-3.11 ± 0.26	1.21 ± 0.06	0.80 (0.00)	$H_1 : \hat{\beta} > 1$	98	0.00
3. Proximal width	100	-1.52 ± 0.29	0.79 ± 0.06	0.69 (0.00)	$H_1 : \hat{\beta} < 1$	98	0.00
4. Distal height	100	-5.07 ± 0.18	1.60 ± 0.04	0.89 (0.00)	$H_1 : \hat{\beta} > 1$	98	0.00
5. Distal width	98[b]	-3.61 ± 0.26	1.08 ± 0.06	0.79 (0.00)	$H_1 : \hat{\beta} \neq 1$	96[b]	0.15*
6. Proximal shaft height	100	-3.30 ± 0.17	1.16 ± 0.04	0.87 (0.00)	$H_1 : \hat{\beta} > 1$	98	0.00
7. Middle shaft height	100	-3.52 ± 0.15	1.17 ± 0.03	0.91 (0.00)	NA	NA	NA
8. Distal shaft height	100	-3.18 ± 0.29	1.05 ± 0.04	0.89 (0.00)	$H_1 : \hat{\beta} \neq 1$	98	0.15*
9. Mass of baculum	100	-14.66 ± 0.29	3.49 ± 0.06	0.94 (0.00)	NA	NA	NA
Total	**100**						

[a] Number of bacula for canine aged animals and animals of unknown-age (the 3 pups were excluded from analysis, i.e., *n* = 100 bacula).

[b] Two distal width measurements were not recorded for PEM2049 and PEM2134.
r, Spearman rank-order correlation coefficient.
All correlations are significant at the 1% level (2-tailed).
NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.
* Since the *p*-value was > 0.05, we cannot reject H_0 in favour of H_1 at the 5% significance level; therefore growth is isometric.

Table 5.9 ***'Robust' least squares straight line equations and Spearman rank-order correlation coefficients for log bacular measurement (mm) on age (y)***

Dependent variable		**Linear regression**		
	n[a]	**Intercept ± S.E.**	**Slope ± S.E.**	***r* (*p*-values)**
1. Length of baculum	37	3.88 ± 0.05	0.10 ± 0.01	0.83 (0.00)
2. Proximal height	37	1.13 ± 0.08	0.15 ± 0.01	0.67 (0.00)
3. Proximal width	37	1.31 ± 0.09	0.11 ± 0.01	0.78 (0.00)
4. Distal height	37	1.10 ± 0.10	0.17 ± 0.01	0.76 (0.00)
5. Distal width	37	0.45 ± 0.07	0.13 ± 0.01	0.68 (0.00)
6. Proximal shaft height	37	1.05 ± 0.06	0.13 ± 0.01	0.74 (0.00)
7. Middle shaft height	37	0.89 ± 0.06	0.13 ± 0.01	0.85 (0.00)
8. Distal shaft height	37	0.82 ± 0.06	0.11 ± 0.01	0.79 (0.00)
9. Mass of baculum	37	-1.28 ± 0.15	0.37 ± 0.02	0.87 (0.00)
Total	**37**			
Standard body length	**26**[b]	4.46 ± 0.04	0.08 ± 0.01	0.83 (0.00)

[a] Number of bacula for canine aged animals (only animals 1–10 y were included in analysis, i.e., *n* = 37 bacula).

[b] SBLs for 11 aged males 1–10 y were not recorded.
r, Spearman rank-order correlation coefficient.
All correlations are significant at the 1% level (2-tailed).
[Model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test for allometry not applicable].

DISCUSSION

Bacular size

In Cape fur seals from the Eastern Cape coast, maximum bacular length was 139.3 mm and mass was 12.5 g; however bacula up to 141 mm (Oosthuizen & Miller, 2000) and 16.8 g (Rand, unpubl. report) have been reported from other areas. Baculum length was similar to that of the northern fur seal (Scheffer, 1950). As with other Otariidae, bacular length was considerably smaller than that of most Phocidae and the Odobenidae (Scheffer & Kenyon, 1963).

Bacular shape

Although detailed information on the morphology of the otariid bacula is sparse, bacular shape was most similar to *Callorhinus* and *Zalophus* (Kim *et al*., 1975; Morejohn, 1975; King, 1983). For example, in *Arctocephalus*, *Callorhinus* and *Zalophus*, the adult bacular apex consists of a dorsal and a ventral knob. When viewed anteriorly, the knobs are parallel sided (*Arctocephalus* and *Zalophus*), or resemble a figure-of-eight (*Callorhinus*).

Apical keels (lateral expansion of the apex) are present on the baculum of some *Zalophus*, yet absent in both *Arctocephalus* and *Callorhinus* (Kim *et al*., 1975; Morejohn, 1975).

Bacular length as an indicator of SBL and age

As with other species of pinnipeds, there is considerable variation in bacular length with age, especially in younger animals (Rand, unpubl. report; Scheffer, 1950; Bester, 1990; Oosthuizen & Miller, 2000).

In male Cape fur seals, bacular length was found to be a ‘rough indicator’ of SBL and age group, but not of absolute age. The classification criteria for age group, and SBL, developed in this study will be particularly useful when canines are not available for age determination; a seal is decomposed/scavenged (total SBL can not be measured); the skull is incomplete/absent (total SBL can not be extrapolated from skull length); or museum records have been misplaced or destroyed. As more specimens become available, the classification criteria will be more precise.

Bacular growth

In male Cape fur seals, growth of the baculum is a differential process with most variables growing rapidly relative to SBL and bacular length. Two variables were isometric and one was negatively allometric, relative to bacular length, indicating that the adult baculum was not simply an enlarged version of the juvenile baculum.

Growth changes in bacular length and mass described in this study generally support findings reported by Oosthuizen & Miller (2000). In this study based primarily on animals collected from the south and south-west coast of southern Africa, growth in bacular length took place rapidly up until 5 y; peaked at 9–10 y; and then slowed. Our findings could not be compared to those of Rand (1956) because, in the latter, age was estimated from cranial suture closure which has subsequently been shown to be an unreliable indicator of absolute age in this species (Stewardson *et al*., 200X*b*).

The biological significance of bacular growth patterns

In male Cape fur seals, a growth spurt in bacular length occurs at 2–3 y (Rand, unpubl. report; Oosthuizen & Miller, 2000), when males attain puberty (Stewardson *et al*., 1998). After puberty, the baculum continues to increase in length with increasing age, approximating full length at about 9 y (Oosthuizen & Miller, 2000; present study). Bacular dimensions, other than length, approximate full size between 8–10 y (present study), when most males have attained full reproductive capacity (present study). Although males can sire offspring at a young age (e.g., at 4 y in captivity; Linda Clokie-Van Zyl, pers. comm.), bacular growth is geared to coincide with the attainment of social maturity, presumably to enhance the effective-ness of copulation.

Socially mature male Cape fur seals: (i) may achieve a high level of polygyny at large colonies (David, 1987); (ii) usually copulate once with each harem female, 5–7 days postpartum during a brief breeding season (November to late December) (David & Rand, 1986); and (iii) usually exhibit brief intromission duration (Stewardson, pers. obs.). In such males, the baculum is therefore large enough to provide sufficient mechanical support for insertion and repeated copulations (with potentially numerous females within a short period of time), and may assist in deeper penetration. The ornate apex presumably serves to stimulate the females vagina (e.g., Eberhard, 1985, 1996); however, considering that: (i) female Cape fur seals are not ‘induced ovulaters’; (ii) copulation occurs when the female is sexually receptive; and (iii) sperm competition is weak, the function of the apex in this species remains unclear.

CONCLUSION

Data presented in this study provide detailed information on the morphology of the Cape fur seal bacula, confirming earlier descriptions given by Mohr (1963) and Rand (1956; unpubl. report). They provide new information on the patterns of bacular growth in relation to age and SBL (Rand, 1956; Oosthuizen & Miller, 2000), and demonstrate that bacular length is a ‘rough indicator’ of SBL and age group, but not of absolute age.

Further studies examining the morphology and growth patterns of the pinniped bacula from known-age animals are required to establish species affinities, and understand the significance of bacular variation in relation to copulatory behaviour and mating systems.

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Appendix 5.1 ***Cape fur seals (n = 103) examined in this study.*** **Animals were collected from the Eastern Cape coast of South Africa between August 1978 and December 1995.**

	ID No.	Date of collection	Approximate location[b]	Method of collection[c]	SBL (cm)
1.	PEM603	2 Aug 78	Bell Buoy, Algoa Bay (AB) (33° 59'S, 25° 42'E)	sci. permit	150
2.	PEM605	4 Apr 79	Riy Bank, AB (34° 00'S, 25° 53'E)	sci. permit	153
3.	PEM607	30 Sep 79	King's Beach, Port Elizabeth (PE) (33° 58'S, 25° 39'E)	rehab. (D)	91
4.	PEM608	29 Aug 79	Cape Recife–Riy Bank, AB (34° 02'S, 25° 42'E – 34° 00'S, 25° 53'E)	sci. permit	182
5.	PEM661	17 July 74	Riy Bank–St. Croix, AB (34° 00'S, 25° 53'E – 33° 48'S, 25° 46'E)	sci. permit	141
6.	PEM670	5 Mar 79	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	158
7.	PEM676	16 Feb 81	NR	oceanarium	197
8.	PEM824	23 Mar 82	Pollock Beach, PE (33° 59'20"S, 25° 40'30"E)	stranding	174
9.	PEM828	26 Mar 82	Port Elizabeth Harbour (33° 58'S, 25° 37'E)	stranding	158
10.	PEM834	21 Apr 82	22 km E of Sundays River Mouth, Woody Cape (WC)	stranding	162
11.	PEM874	18 Oct 82	32 km E of Sundays River Mouth, WC	stranding	157
12.	PEM877	2 Oct 82	E of Swartkops River Mouth, AB	stranding	165
13.	PEM888	2 Nov 82	7 km E of Kasuga River Mouth, Port Alfred (PA)	stranding	212
14.	PEM889	2 Nov 82	4 km E of Kasuga River Mouth, PA	stranding	138
15.	PEM898	22 Dec 82	1 km E of Van Starden's River Mouth, St. Francis Bay (FB)	stranding	200
16.	PEM916	Jan 1983	Willows, PE (34° 03'S, 25° 35'E)	stranding	91
17.	PEM917	11 Jan 83	2 km W of Maitland River Mouth, FB	stranding	104
18.	PEM928	14 Mar 82	28 km E of Sundays River Mouth, WC	stranding	140
19.	PEM951	16 May 83	35 km E of Sundays River Mouth, WC	stranding	170
20.	PEM952[a]	22 Feb 80	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	243
21.	PEM958	13 Dec 83	Humewood, PE (33° 59'S, 25° 40'E)	other	190
22.	PEM1073	12 Sep 84	Oyster Bay (34° 10'S, 24° 39'E)	stranding	133
23.	PEM1143	11 Mar 85	7 km E of Swarkops River Mouth	stranding	208
24.	PEM1214	28 Aug 85	Cape Recife, PE (34° 02'S, 25° 42'E)	stranding	165
25.	PEM1453	30 Jan 88	3 km E Kabeljous River Mouth, Jeffreys Bay	stranding	193
26.	PEM1507	5 Feb 88	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	198
27.	PEM1587	18 May 89	Amsterdamhoek (33° 52'S, 25° 38'E)	stranding	192
28.	PEM1706	12 July 90	1.5 km E of Sundays River Mouth, WC	stranding	126
29.	PEM1868	24 Sep 91	Cape Recife, PE (34° 02'S, 25° 42'E), near lighthouse	stranding	199
30.	PEM1882	6 May 92	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	180
31.	PEM1890	13 July 92	Cape Recife, PE (34° 02'S, 25° 42'E)	stranding	192
32.	PEM1891	18 July 92	Hobie Beach, PE (33° 58'50"S, 25° 39' 30"E)	rehab. (D)	137
33.	PEM1892	27 July 92	Sardinia Bay (34° 02'S, 25° 29'E), 800 m E of boat shed	stranding	185
34.	PEM1895	29 July 92	Cape Recife, PE (34° 02'S, 25° 42'E), 2 km E of lighthouse	stranding	188
35.	PEM1900	July 92	NR	rehab. (D)	92
36.	PEM1901	July 92	Jefferys Bay (34° 03' S, 24° 55'E)	rehab. (D)	84
37.	PEM1999	20 July 92	EC trawl grounds (34° 52'S, 23° 35'E–34° 50'S, 23° 48'E)	by-catch	–
38.	PEM2000	21 July 92	EC trawl grounds (34° 50'S, 23° 48'E–34° 48'S, 24° 00'E)	by-catch	–
39.	PEM2001	21 July 92	EC trawl grounds (34° 50'S, 23° 48'E–34° 48'S, 24° 00'E)	by-catch	–
40.	PEM2002	22 July 92	EC trawl grounds (34° 55'S, 23° 14'E–34° 53'S, 23° 26'E)	by-catch	–
41.	PEM2003	24 July 92	EC trawl grounds (34° 51'S, 23° 42'E–34° 49'S, 23° 53'E)	by-catch	–
42.	PEM2004	25 July 92	EC trawl grounds (34° 45'S, 24° 18'E–34° 48'S, 24° 00'E)	by-catch	–
43.	PEM2005	11 Aug 92	EC trawl grounds (34° 43'S, 24° 34'E–34° 40'S, 24° 45'E)	by-catch	–
44.	PEM2006	13 Aug 92	EC trawl grounds 34° 45'S, 24° 25'E–34° 42'S, 24° 40'E)	by-catch	–
45.	PEM2007	14 Aug 92	EC trawl grounds (34° 42'S, 24° 51'E–34° 42'S, 24° 42'E)	by-catch	–
46.	PEM2008	14 Aug 92	EC trawl grounds (34° 41'S, 24° 42'E–34° 38'S, 24° 54'E)	by-catch	–
47.	PEM2009	22 Aug 92	EC trawl grounds (34° 41'S, 24° 45'E–34° 37'S, 24° 59'E)	by-catch	–
48.	PEM2010	22 Aug 92	EC trawl grounds (34° 47'S, 24° 11'E–34° 46'S, 24° 25'E)	by-catch	–
49.	PEM2011	8 Sep 92	EC trawl grounds (33° 50'S, 27° 06'E–34° 37'S, 24° 59'E)	by-catch	–
50.	PEM2014	25 Sep 92	EC trawl grounds (34° 23'S, 26° 04'E–34° 23'S, 25° 58'E)	by-catch	–
51.	PEM2018	25 Jan 93	Bird Island, AB (33° 51'S, 26° 17'E)	stranding	155
52.	PEM2020	28 Jan 93	Kenton-On-Sea (33° 40'S, 26° 40'E)	euthanased	66
53.	PEM2024	30 Jan 93	Woody Cape, AB (33° 46'S, 26° 19'E)	euthanased	74
54.	PEM2035	11 Mar 93	The Pipes, SE of Pollock Beach (33° 59'20"S, 25° 40' 30"E)	stranding	118
55.	PEM2044	28 May 93	Seaview (34° 01'S, 25° 17'E), Otter Pools	stranding	206
56.	PEM2045	30 May 93	Schoenmakerskop (34° 02'S, 25° 32'E)	stranding	145
57.	PEM2046	19 May 93	EC trawl grounds (35° 09'S, 21° 28'E)	by-catch	141
58.	PEM2047	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	by-catch	167

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	ID No.	Date of collection	Approximate location[b]	Method of collection[c]	SBL (cm)
59.	PEM2048	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	by-catch	157
60.	PEM2049	7 June 93	Kini Bay (34° 01'S, 25° 26'E), Western Beach	stranding	174
61.	PEM2051	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	by-catch	168
62.	PEM2052	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	by-catch	171
63.	PEM2053	28 June 93	EC trawl grounds (34° 46'S, 24° 21'E–34° 44'S, 24° 32'E)	by-catch	153
64.	PEM2054	29 June 93	EC trawl grounds (34° 45'S, 24° 28'E–34° 47'S, 24° 18'E)	by-catch	165
65.	PEM2055	29 June 93	EC trawl grounds (34° 46'S, 24° 22'E–34° 44'S, 24° 32'E)	by-catch	179
66.	PEM2056	29 June 93	EC trawl grounds (34° 46'S, 24° 22'E–34° 44'S, 24° 32'E)	by-catch	139
67.	PEM2057	30 June 93	Pollock Beach, PE (33° 59'20"S, 25° 40'30"E)	rehab. (D)	172
68.	PEM2081	19 July 93	Cape Recife, PE (34° 02'S, 25° 42'E)	stranding	162
69.	PEM2082	July 93	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	176
70.	PEM2087	17 Aug 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	stranding	190
71.	PEM2131	13 Dec 93	Sundays River Mouth, AB	rehab. (D)	67
72.	PEM2134	28 Dec 93	Noordhoek (34° 02'S, 25° 39'E)	stranding	216
73.	PEM2137	5 Jan 94	Summerstrand, PE (34° 00'S, 25° 42'E)	rehab. (D)	118
74.	PEM2140	17 Jan 94	40 km E of Sundays River Mouth, WC	stranding	187
75.	PEM2141	17 Jan 94	39 km E of Sundays River Mouth, WC	stranding	198
76.	PEM2155	11 Feb 94	10 km E of Sundays River Mouth, WC	stranding	184
77.	PEM2186	7 Apr 94	Amsterdamhoek (33° 52'S, 25° 38'E)	rehab. (D)	90
78.	PEM2188	17 Apr 94	NR	oceanarium	132
79.	PEM2191	4 May 94	Port Alfred (33° 36'S, 26° 55'E)	euthanased	100
80.	PEM2194	2 June 94	Schoenmakerskop (34° 02'S, 25° 32'E)	stranding	194
81.	PEM2198	July 94	Plettenberg Bay (34° 03'S, 23° 24'E)	stranding	105
82.	PEM2203	18 July 94	Port Elizabeth Harbour (33° 58'S, 25° 37'E)	other	204
83.	PEM2238[d]	1994	Durban (29° 50'S, 31° 00'E)	rehab. (D)	96
84.	PEM2248	12 Aug 94	Seaview (34° 01'S, 25° 27'E)	stranding	158
85.	PEM2252	22 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	172
86.	PEM2253	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	152
87.	PEM2254	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	146
88.	PEM2256	17 Sep 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	198
89.	PEM2257B	8 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	170
90.	PEM2348	14 Nov 94	Humewood, PE (33° 59'S, 25° 40'E)	stranding	189
91.	PEM2359	21 Feb 95	Sundays River Mouth, AB	stranding	108
92.	PEM2374	24 Mar 95	Jeffreys Bay (34° 03'S, 24° 55'E)	stranding	186
93.	PEM2379	12 Apr 95	Bokness (33° 41'S, 26° 31'E)	stranding	189
94.	PEM2400	13 July 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	176
95.	PEM2403	July 95	NR	rehab. (D)	88
96.	PEM2404	July 95	NR	rehab. (D)	92
97.	PEM2405	July 95	NR	rehab. (D)	87
98.	PEM2406	July 95	Swartkops River Mouth	stranding	154
99.	PEM2411	24 Aug 95	Plettenberg Bay (34° 03'S, 23° 24'E)	by-catch	155
100.	PEM2414	25 Aug 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	148
101.	PEM2415	27 Aug 95	Sardinia Bay (34° 02'S, 25° 29'E)	stranding	130
102.	PEM2454	8 Nov 95	Noordhoek (34° 02'S, 25° 39'E)	stranding	196
103.	PEM2458	3 Dec 95	Cape St. Francis (34° 12'S, 24° 52'E)	rehab. (D)	110

[a] Animal collected in 1980 and issued with a new identification number in 1983, i.e., PEM952.

[b] Kabeljous River Mouth (34° 00'S, 24° 56'E); Maitland River Mouth (33° 59'S, 25° 18'E); Sundays River Mouth (33° 43'S, 25° 51'E); and Van Starden's River Mouth (33° 58'S, 25° 13'E).

[c] Stranding, animal washed up dead on beach (n = 47). By-catch, animal incidentally caught in a commercial trawl net during fishing operations (n = 32). Rehab. (D), animal died during rehabilitation at the Port Elizabeth Oceanarium (n = 13). Euthanased, animal suffering from illness/injury and was put down to prevent further suffering (n = 3). Sci. permit, animal collected under scientific permit (n = 4). Oceanarium, captive animal of the Port Elizabeth Oceanarium (n = 2, PEM676, Tommy; PEM2188, Rascal). Other, animal died from other causes (n = 2, PEM958 found floating in the ocean off Humewood Beach; PEM2203 stoned to death by fisherman).

[d] Animal PEM2238 collected NE of the Eastern Cape, i.e., Durban (29° 50'S, 31° 00'E).

NR, not recorded.

CHAPTER 6

Suture age as an indicator of physiological age in the male Cape fur seal, *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae)

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ABSTRACT

In this study we examine suture age as an indicator of physiological age in the male Cape fur seal, *Arctocephalus pusillus pusillus*, from the coast of southern Africa. We describe the sequence of cranial suture closure ($n = 11$ sutures), determine whether suture age corresponds to chronological age, and estimate asymptotic size from suture age using nonlinear growth models (logistic, von Bertalanffy, Gompertz) fitted to cross-sectional morphometric data ($n = 10$ variables). Animals ($n = 68$ males) ranged in age from < 1 mo to ≥ 12 y (80 to 201 cm). Nineteen animals were of known-age (animals tagged as pups), 45 were aged from incremental lines observed in the dentine of upper canines and 4 were not aged. The sequence of partial suture closure differed from the sequence of full suture closure, with fusion beginning at different ages and some sutures taking longer to close than others. In animals ≤ 12 y, the sequence of full suture closure was the basioccipito-basisphenoid, occipito-parietal, interparietal/coronal and finally the squamosal-jugal. Suture age was found to be an unreliable indicator of chronological age. However, the basioccipito-basisphenoid can be used independently as an indicator of age, i.e., suture open = male ≤ 3 y old; suture fully closed = male 3–4 y or older and male has reached puberty. Asymptotic size estimates for 10 morphological measurements inferred from suture age are documented, and where possible, compared to asymptotes derived from chronological age.

Key words: Pinnipeds, Otariidae, suture age, asymptotic size

INTRODUCTION

Age determination in pinnipeds is important in many biological studies, particularly those examining development and growth. Various techniques have been used to determine absolute and relative age in pinnipeds. Techniques include: examination of tooth structure, the use of incremental structures in nails and bones, suture closure, standard body length, baculum development, eye lens weight, ovarian structure, and pelage characteristics (see Laws, 1962; Jonsgard, 1969; Morris, 1972; McCann, 1993 for reviews). Currently, examination of tooth structure is the most precise method of age determination in pinnipeds (Scheffer, 1950; Laws, 1953; McCann, 1993). In the majority of species however, the pulp cavity closes at some stage which terminates tooth growth (McCann, 1993).

In *Arctocephalus pusillus pusillus*, Cape fur seal, it is not possible to determine chronological age of animals > 13 y from examination of tooth structure because of pulp cavity closure. Examination of growth and development of the skeleton (physiological age) is thought to be one of the more useful methods of estimating relative age in older specimens (e.g., Rand, 1949, 1956). It has been suggested that in marine mammals, physical development may be better correlated with parameters which indicate the individual's proximity to physical maturity than with fixed morphometric values such as chronological age (Hui, 1979). In pinnipeds, cross-sectional data is typically used for growth studies. If growth patterns have been unchanged over the lifetime of the oldest animal, then the fitted growth curve will estimate the average of the growth curves of individual animals. This assumption is known as stationarity. However, many pinnipeds have been subject to periodic harvest and compete with a growing fishing industry. When the effects of anthropogenic activity on pinniped populations are taken into consideration, it is probable that 'individual' growth rates and patterns are indistinct when values are averaged using this method. Change in growth will take place at a slower or faster rate than is the case for an 'individual' (Sinclair, 1973; Hui, 1979).

Here we use suture closure (suture age) as an indicator of physiological age in the male Cape fur seal. Specific objectives were to: (i) describe the sequence of cranial suture closure, (ii) determine whether suture age corresponds to chronological age, and (iii) estimate asymptotic size inferred from suture age using nonlinear growth models fitted to cross-sectional morphometric data.

MATERIALS AND METHODS

Collection of specimens and morphometry

Male Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). Collection procedures followed Stewardson *et al.*, 200X*a*, *b*, *c*. From this collection, 49 males were selected for examination, i.e., external body (*n* = 45 males), skull (*n* = 42 males) and bacular (*n* = 35 males) measurements.

The sample was supplemented with external body and skull measurements from 19 known-age animals (animals tagged as pups) from Marine and Coastal Management (MCM), Cape Town.

Animals (*n* = 68 males) ranged in age from < 1 mo to ≥ 12 y[1], with standard body lengths ranging from 80 to 201 cm. Nineteen animals were of known-age, 45 were aged from incremental lines observed in the dentine of upper canines (Stewardson *et al.*, 200X*a*), and 4 were not aged.

The following measurements were examined: external body (standard body length, tip of snout to genital opening, tip of snout to anterior insertion of front flipper, length of front flipper, length of hind flipper), skull (condylobasal length, bizygomatic breadth, mastoid breadth, length of mandible) and baculum (bacular length). Measurements were recorded according to Stewardson *et al.*, (200X*a*, *b*, *c*).

Sequence of suture closure

Eleven cranial sutures (Table 6.2) from 21 known-age skulls, and 45 canine aged skulls, were examined and assigned a value of 1–4, according to the degree of closure (1 = suture fully open; 2 = suture less than half-closed; 3 = suture more than half-closed; and 4 = suture completely closed) following Stewardson *et al.*, (200X*b*). These values were added to give a total suture index (SI), ranging from 11 (all sutures open) to 44 (all sutures closed).

Asymptotic size

Asymptotic size, inferred from suture age, was estimated by fitting three nonlinear growth curves (Table 6.1) to cross-sectional morphometric data (Table 6.5). Constrained nonlinear optimisation, using the Sequential Quadratic Programming algorithm, was used to estimate the parameters in each growth model. The residual sum of squares was used as the loss function. The nonlinear growth curves were fitted using SPSS (SPSS Inc., Chicago, Illinois, 1989-1999, 9.0.1).

RESULTS

Suture closure and chronological age

The relationship between suture age and chronological age (Fig. 6.1, Table 6.2, 6.4) was examined using known-age animals, 10 mo to 12 y (*n* = 21 males).

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[1] In Cape fur seals, animals > 13 y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes which terminates tooth growth, hence the age group '≥12 y'. Estimated longevity is *c.* 20 y.

Table 6.1 *Growth models fitted to cross-sectional morphometric data for male Cape fur seals*

Model	**Equation**	**References**
Logistic	$y = \dfrac{a}{1 + b\exp(-cx)}$	Batschelet (1975); Innes *et al.,* (1981)
Gompertz	$y = a\exp(-b\exp(-cx))$	Laird (1966); Innes *et al.,* (1981)
von Bertalanffy	$y = a(1 - b\exp(-cx))^3$	Turner *et al.,* (1976); Innes *et al.,* (1981)

a, asymptote (line tangent to the curve at infinity).
b & c, fitted constants.
$\exp(x) = e^x$, where e is the base of the natural logarithms.

The sequence of partial suture closure (PSC) differed from the sequence of full suture closure (FSC) with fusion beginning at different ages and some sutures taking longer to close than others.

For the range of available specimens, the sequence of PSC according to chronological age was coronal (PSC at 2 y), occipito-parietal (PSC at 3 y), interparietal (PSC at 4 y), squamosal-jugal (PSC at 7 y) and premaxillary-maxillary (PSC at 12 y). Considering that the basioccipito-basisphenoid was fully closed at 3–4 y, PSC would occur at 1 or 2 y, before or at the same time as the coronal. The squamosal-parietal, interfrontal, basisphenoid-presphenoid (sutures of the brain case), internasal and maxillary (sutures of the face), showed no signs of partial closure in animals ≤ 12 y.

The sequence of FSC according to chronological age was basioccipito-basisphenoid, occipito-parietal, interparietal/coronal and finally squamosal-jugal. With the exception of the squamosal-jugal these are sutures of the brain case. The basioccipito-basisphenoid was fully closed at 3–4 y. The occipito-parietal was fully closed in some animals as early as 5 y. The interparietal was fully closed in one 9-y-old and one 12-y-old. The coronal was fully closed in one 9-y-old and one 12-y-old. The squamosal-jugal was fully closed in one 12-y-old.

Although the sutures and their pattern of closure were clearly related to each other, the relationship

Table 6.2 *Suture index for male Cape fur seals according to chronological age (y) and age group (known-age animals tagged as pups)*

No.[a]	**Suture**[b]	**Yearling**	**Subadults**						**Adults**	
		10 mo	2 y	3 y	4 y	5 y	6 y	7 y	9 y	12 y
vii.	**Basioccipito-basisphenoid** (brain case)	1	1	**4**	**1[d]–4**	**4**	**4**	**4**	**4**	**4**
i.	**Occipito-parietal** (brain case)	1	1	3	2–3	**4**	**3–4**	**3**	**4**	**4**
ii.	**Interparietal** (brain case)	1	1	1	1–2	1–2	1–3	2	**4**	**4**
iii.	**Coronal** (brain case)	1	1–2	2	2–3	2	2–3	2	**4**	**4**
x.	**Squamosal-jugal** (face-zygomatic)	1	1	1	1	1	1	1–2	1	**4**
vi.	**Premaxillary-maxillary** (face-maxilla)	1	1	1	1	1	1	1	1	2
xi.	**Maxillary** (face-maxilla)	1	1	1	1	1	1	1	1	1
ix.	**Squamosal-parietal** (brain case)	1	1	1	1	1	1	1	1	1
iv.	**Interfrontal** (brain case)	1	1	1	1	1	1	1	1	1
viii.	**Basisphenoid-presphenoid** (brain case)	1	1	1	1	1	1	1	1	1
v.	**Internasal** (face-nasal)	1	1	1	1	1	1	1	1	1
	Suture index[c]	11	11–12	17	13–19	18–19	18–21	18–19	23	27
	Total no. skulls = 21	**2**	**2**	**2**	**6**	**2**	**3**	**2**	**1**	**1**

[a] Suture numbers i–xi correspond to Fig.2 in Stewardson *et al.*, (200X*b*).
[b] Sutures arranged in order of closure (1, suture fully open; 2, suture less than half-closed; 3, suture more than half-closed; 4, suture completely closed).
[c] Total value of the 11 cranial sutures (minimum and maximum). Note that the suture index is not necessarily the total value of each column.
[d] The basioccipito-basisphenoid was fully open in one 4-y-old (AP4496).

Table 6.3 *Suture index for male Cape fur seals according to standard body length*

		Standard body length (cm)												
No.[a]	**Suture**[b]	**80–90**	**91–100**	**101–110**	**111–120**	**121–130**	**131–140**	**141–150**	**151–160**	**161–170**	**171–180**	**181–190**	**191–200**	**201**
vii.	**Basioccipito-basisphenoid** (brain case)	1	**1–4**	**2–4**	**1–4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**
i.	**Occipito-parietal** (brain case)	1	1	1–2	2–3	3	**4**	**3–4**	**3–4**	**3–4**	**4**	**4**	**4**	**4**
ii.	**Interparietal** (brain case)	1	1	1	1	1	1–2	**1–4**	**1–3**	**1–4**	**1–4**	**2–4**	**1–4**	**4**
iii.	**Coronal** (brain case)	1	1–2	1–2	2	2	1–2	1–3	2–3	**1–4**	**3–4**	**2–4**	**2–4**	**2**
x.	**Squamosal-jugal** (face-zygomatic)	1	1	1	1–2	1	1	1–2	1	1	**1–4**	**1–4**	**1–4**	**1**
xi.	**Maxillary** (face-maxilla)	1	1	1	1	1	1	1	1	1	1	1–3	**1–4**	**1**
vi.	**Premaxillary-maxillary** (face-maxilla)	1	1	1	1	1	1	1	1	1	1–2	1–3	1–3	1
ix.	**Squamosal-parietal** (brain case)	1	1	1	1	1	1	1	1	1	1–2	1–3	1–3	1
iv.	**Interfrontal** (brain case)	1	1	1	1	1	1	1	1	1	1–2	1–2	1–3	1
viii.	**Basisphenoid-presphenoid** (brain case)	1	1	1	1	1	1	1	1	1	1	1	1–2	1
v.	**Internasal** (face-nasal)	1	1	1	1	1	1	1	1	1	1	1	1–2	1
	Suture index[c]	11	12–14	13–16	13–17	17	17–19	17–21	18–21	17–23	19–27	20–33	18–33	21
	Total no. skulls = 65	**3**	**3**	**4**	**3**	**3**	**2**	**10**	**7**	**8**	**6**	**6**	**9**	**1**

[a] Suture numbers i–xi correspond to Fig.2 in Stewardson *et al.*, (200X*b*).

[b] Sutures arranged in order of closure (1, suture fully open; 2, suture less than half-closed; 3, suture more than half-closed; 4, suture completely closed).

[c] Total value of the 11 cranial sutures (minimum and maximum). Note that the suture index is not necessarily the total value of each column.

Table 6.4 *Total suture score for ages 10 mo to 12 y showing age range in months, mean age ± S.E. and C.V. (known-age animals tagged as pups)*

Suture score	*n*	Age range (mo)	Mean age ± S.E. (mo)	C.V.
11	3	10–22	14.0 ± 4.0	49.5
12	1	20	20.0	–
13	1	46	46.0	–
16	1	46	46.0	–
17	4	34–47	41.5 ± 3.1	14.8
18	4	53–80	66.8 ± 5.5	16.6
19	4	53–80	66.3 ± 6.2	18.7
21	1	74	74.0	–
23	1	106	106.0	–
27	1	143	143.0	–
	21			

Where sample size is one, we cannot calculate S.E. of the mean or C.V.

was not sufficiently close to be used as a reliable technique for estimating chronological age (Table 6.4). The standardised residuals versus fitted values plots exhibited curvature; therefore, the straight line does not adequately describe the relationship between suture age and chronological age.

Suture closure and standard body length

The relationship between suture age and SBL (Table 6.3) was examined using animals 80–201 cm, 10 m to ≥ 12 y. SBL was not recorded for 3 animals (*n* = 65 males).

For the range of available specimens, the sequence of PSC according to SBL was basioccipito-basisphenoid, occipito-parietal/coronal, squamosal-jugal, interparietal, premaxillary-maxillary/squamosal-parietal/interfrontal, maxillary and finally the basisphenoid-presphenoid/internasal.

The sequence of FSC was basioccipito-basisphenoid, occipito-parietal, interparietal, coronal, squamosal-jugal and finally the maxillary. The basioccipito-basisphenoid was fully closed in all animals ≥ 118 cm, with FSC evident in some animals ≥ 96 cm. The occipito-parietal was fully closed in all animals ≥ 168 cm, with FSC evident in some animals ≥ 134 cm. The interparietal, coronal, squamosal-jugal and the maxillary were closed in some animals at 141, 170, 173 and 192 cm, respectively. The premaxillary-maxillary, squamosal-parietal, interfrontal, basisphenoid-presphenoid and internasal did not fully close in animals ≤ 201 cm.

Asymptotic size

Estimated asymptotic size was calculated using animals 80–201 cm, 10 m to ≥ 12 y (*n* = 65 males).

Parameters for the three growth functions are given in Table 6.5. Inspection of the residuals versus fitted values plots indicated that the three models were adequate for the range of values available. In terms of the R^2 (a goodness of fit statistic), the models were found to be quite similar. These models adequately described the ‘general’ growth pattern of the 10 variables for suture ages 11–33 (Fig. 6.2–6.11). The von Bertalanffy model for bacular length was the only exception. Asymptotic size derived from the latter was not considered to be reliable.

The logistic model gave consistently smaller asymptotic estimates than the other two growth models, and generally fell within the range of mean value for adults, and the maximum value for adults, reported in this study. Estimated asymptotic size was slightly larger than the maximum adult value for tip of snout to anterior insertion of front flipper, bizygomatic breadth and mastoid breadth (Table 6.5).

The von Bertalanffy model gave a slightly larger estimate than the Gompertz model. Asymptotic size estimates were similar for 8 of the 10 variables. Exceptions were standard body length (11 cm difference) and tip of snout to insertion of front flipper (9 cm difference). Estimates were similar to or slightly larger than the maximum value for adults reported in this study.

Asymptotic estimates derived from suture age were compared with those derived from chronological age to see if asymptotes were similar. The chronological age data did not have animals > 12 y (unable to canine age animals > 13 y), where as the suture age data contained animals > 12 y. Growth continued in most variables beyond 12 y. Therefore, there was insufficient information about the upper limits of the curves to estimate asymptotic size (y), preventing comparison with asymptotes derived from suture age. Bacular length and mandibular length were the only exceptions.

Growth in bacular length slowed in animals at *c.* 10 y, forcing the curve to plateau, providing sufficient information about the upper limits of the curve. Asymptotic size for bacular length derived from measurements based on suture age (logistic 119.1 mm; Gompertz 120.2 mm) was found to be very similar to asymptotic size derived from measurements based on chronological age (logistic 119.9 mm; Gompertz 124.2 mm) (Table 6.5).

Growth in mandibular length also slowed in animals at *c.* 10 y. Asymptotic size for mandibular length derived from measurements based on suture age (logistic 192.1 mm; Gompertz 196.0 mm; Von Bertalanffy 198.0 mm) was found to be very similar to asymptotic size derived from measurements based on chronological age (logistic 190.1 mm; Gompertz 196.1 mm; Von Bertalanffy 198.9 mm) (Table 6.5).

Table 6.5 *Growth parameters (mean ± asymptotic S.E.) of three growth models fitted to cross-sectional morphometric data for male Cape fur seals inferred from suture age*

Growth model	Parameters of growth curves					Adults only[a]	
	a	b	c	R^2	*n*	Mean value	Max. value
External body (cm)							
Standard body length					63	199 ± 3.6	201
Logistic	199.79 ± 6.39	16.13 ± 5.66	0.21 ± 0.03	82%		(*n* = 17)	
Gompertz	204.54 ± 8.05	5.63 ± 1.61	0.16 ± 0.02	81%			
Von Bertalanffy	215.18 ± 11.75	1.00 ± 0.25	0.12 ± 0.02	80%			
Tip of snout to genital opening					45	171.1 ± 3.4	184.0
Logistic	181.41 ± 12.31	11.34 ± 3.36	0.18 ± 0.03	85%		(*n* = 7)	
Gompertz	190.68 ± 17.08	3.99 ± 0.99	0.12 ± 0.03	84%			
Von Bertalanffy	195.46 ± 19.90	0.95 ± 0.23	0.11 ± 0.02	84%			
Tip of snout to anterior insertion of front flipper					45	94.2 ± 3.1	110.0
Logistic	115.15 ± 13.36	12.61 ± 4.61	0.16 ± 0.03	76%		(*n* = 7)	
Gompertz	128.94 ± 23.32	3.71 ± 0.99	0.09 ± 0.03	75%			
Von Bertalanffy	137.66 ± 31.11	0.84 ± 0.20	0.08 ± 0.03	75%			
Length of front flipper					45	47.2 ± 1.9	55.0
Logistic	53.11 ± 6.72	5.87 ± 1.56	0.12 ± 0.03	75%		(*n* = 8)	
Gompertz	58.02 ± 10.72	2.47 ± 0.51	0.08 ± 0.03	75%			
Von Bertalanffy	60.80 ± 13.45	0.62 ± 0.12	0.07 ± 0.03	75%			
Length of hind flipper					44	28.7 ± 0.9	32.0
Logistic	32.04 ± 3.34	6.48 ± 2.77	0.15 ± 0.04	66%		(*n* = 7)	
Gompertz	33.33 ± 4.52	2.84 ± 1.04	0.11 ± 0.04	66%			
Von Bertalanffy	33.95 ± 5.16	0.73 ± 0.26	0.09 ± 0.04	66%			
Skull (mm)							
Condylobasal length					61	253.9 ± 2.6	275.4
Logistic	269.48 ± 5.57	4.36 ± 0.87	0.17 ± 0.02	89%		(*n* = 14)	
Gompertz	273.19 ± 6.66	2.45 ± 0.44	0.14 ± 0.02	89%			
Von Bertalanffy	274.75 ± 7.16	0.68 ± 0.12	0.13 ± 0.02	89%			
Bizygomatic breadth					61	149.1 ± 2.0	158.9
Logistic	165.68 ± 7.37	3.83 ± 0.81	0.13 ± 0.02	84%		(*n* = 14)	
Gompertz	171.50 ± 9.98	2.01 ± 0.36	0.09 ± 0.02	84%			
Von Bertalanffy	174.22 ± 11.33	0.54 ± 0.09	0.09 ± 0.02	84%			
Mastoid breadth					59	137.5 ± 6.0	149.7
Logistic	153.18 ± 5.36	5.26 ± 1.06	0.15 ± 0.02	88%		(*n* = 14)	
Gompertz	158.22 ± 7.15	2.53 ± 0.43	0.11 ± 0.02	88%			
Von Bertalanffy	160.59 ± 8.09	0.67 ± 0.11	0.09 ± 0.02	88%			
Length of mandible[b]					60	191.5 ± 2.9	194.1
Logistic	192.14 ± 5.16	5.76 ± 1.32	0.17 ± 0.02	87%	*(50)*	(*n* = 13)	
	(190.06 ± 9.62)	*(1.13 ± 0.10)*	*(0.26 ± 0.05)*	*(86%)*			
Gompertz	195.96 ± 6.41	2.88 ± 0.58	0.13 ± 0.02	87%			
	(196.08 ± 12.54)	*(0.81 ± 0.05)*	*(0.20 ± 0.05)*	*(86%)*			
Von Bertalanffy	197.65 ± 7.01	0.77 ± 0.15	0.12 ± 0.02	87%			
	(198.85 ± 14.02)	*(0.24 ± 0.01)*	*(0.18 ± 0.05)*	*(86%)*			
Baculum (mm)							
Bacular length[b]					35	112.1 ± 6.4	139.3
Logistic	119.10 ± 2.96	743.85 ± 683.54	0.47 ± 0.06	86%	(40)	(*n* = 14)	
	(119.89 ± 4.89)	*(2.51 ± 0.28)*	*(0.42 ± 0.06)*	*(93%)*			
Gompertz	120.19 ± 3.32	111.26± 82.91	0.36 ± 0.05	85%			
	(124.19 ± 6.59)	*(1.35 ± 0.09)*	*(0.30 ± 0.05)*	*(93%)*			
Von Bertalanffy[c]	–	–	–	–			

R^2, 1 – residual SS/Total corrected SS (where SS is the sum of squares).

[a] Mean value for adults and maximum value is derived from Stewardson *et al.*, (200X*a*, *b*, *c*) and includes males ≥ 7 y 7 mo and unaged males > 200 cm.

[b] Estimated asymptotic size derived from chronological age given in round brackets and italics.

[c] The von Bertalanffy model for bacular length did not fit the data as well as the other two models; asymptotic size derived from this model was not considered to be reliable.

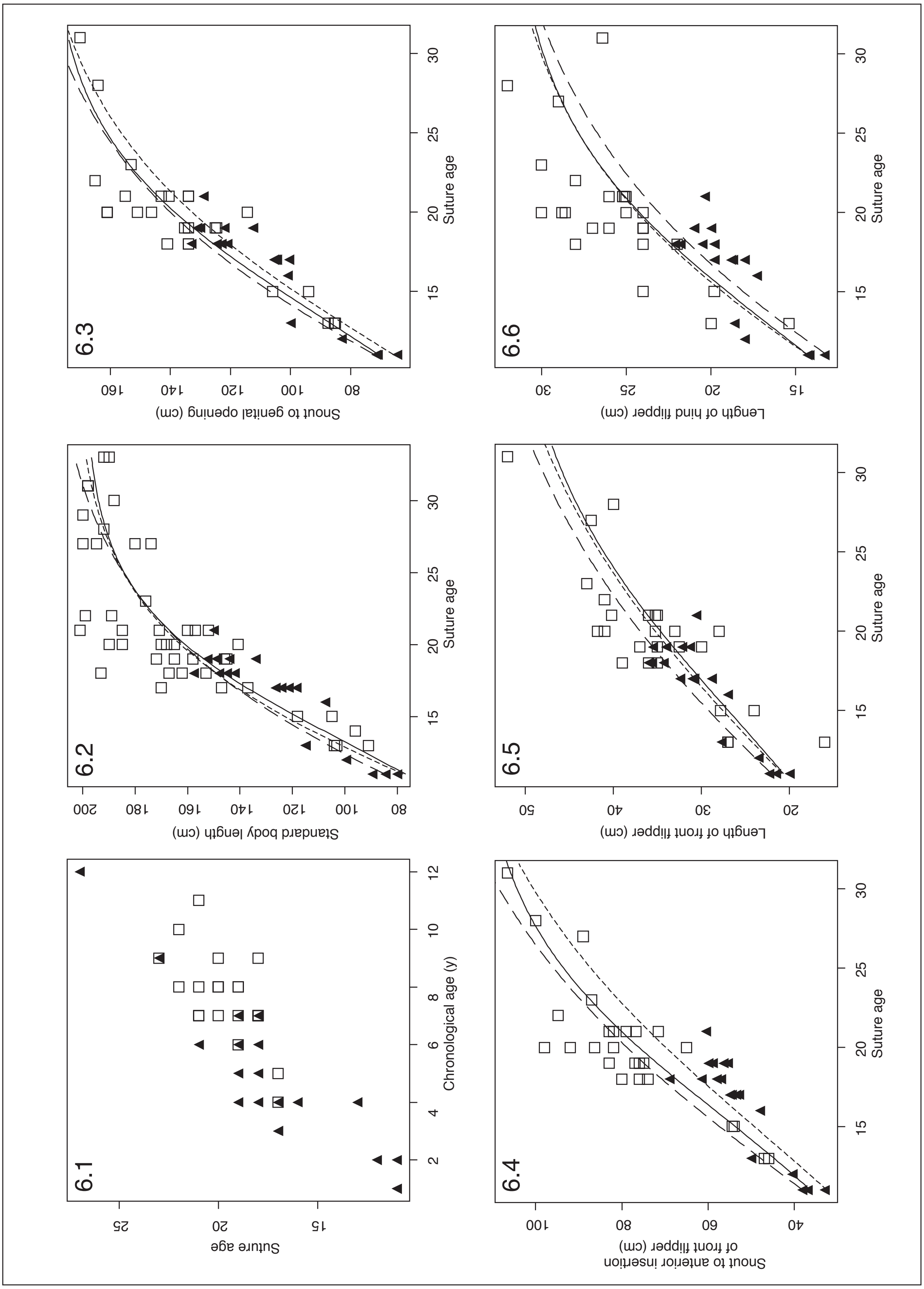

Fig. 6.1–6.6 Bivariate plot of: (1) suture age on chronological age (y) (*n* = 21 MCM known-age animals and *n* = 21 canine aged PEM animals); (2) Seal body length (cm) on suture age; (3) Tip of snout to genital opening (cm) on suture age; (4) Tip of snout to insertion of front flipper (cm) on suture age; (5) Length of front flipper (cm) on suture age; (6) Length of hind flipper (cm) on suture age.

Squares, canine aged animals. Solid triangles, known-age animals (animals tagged as pups). __ __ __ = von Bertalanffy growth model; _ _ _ _ = Gompertz growth model; __ = Logistic growth model.

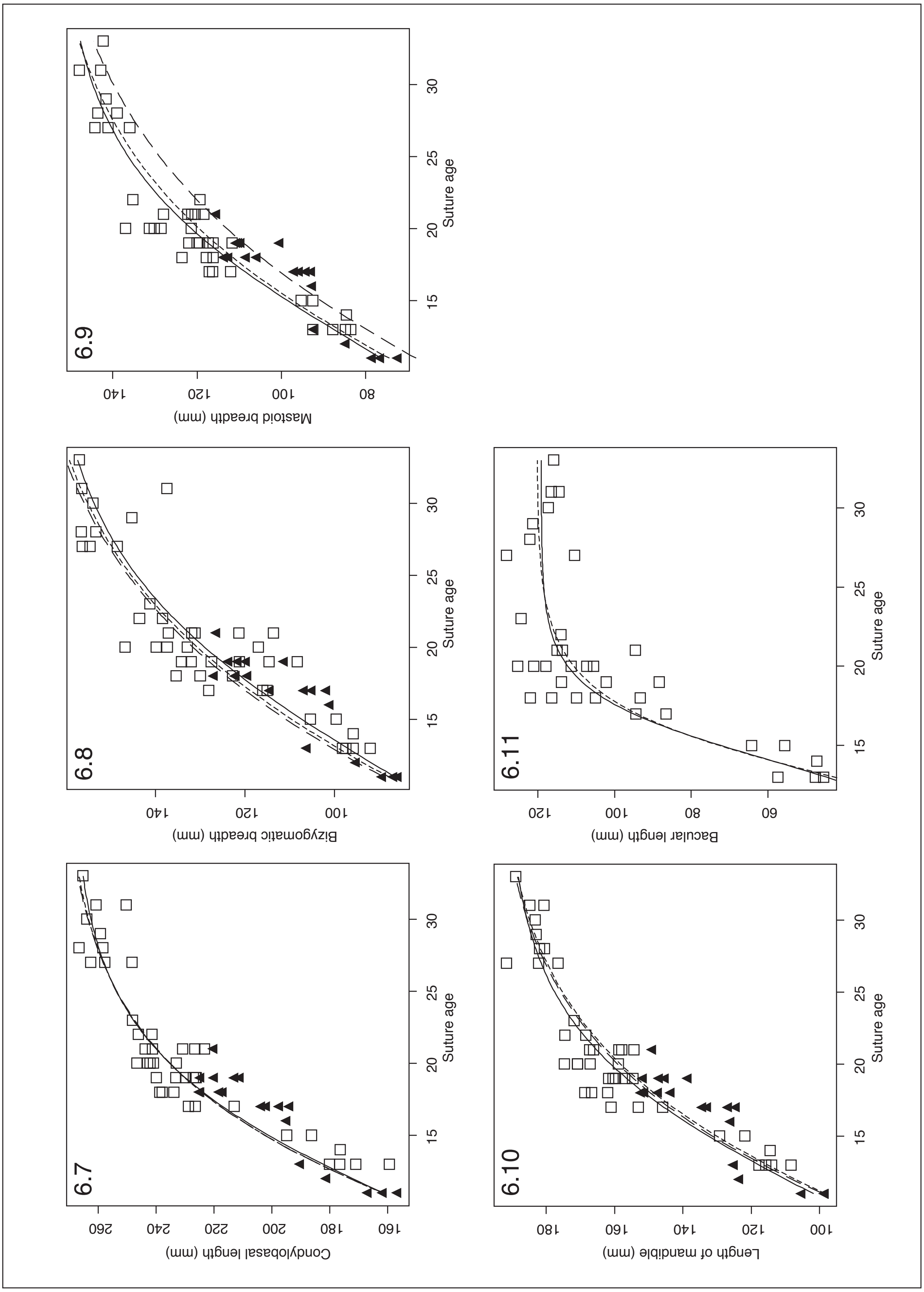

Fig. 6.7–6.11 Bivariate plot of: (7) condylobasal length (cm) on suture age; (8) Zygomatic breadth (cm) on suture age; (9) Mastoid breadth (cm) on suture age; (10) Length of mandible (cm) on suture age; (11) Bacular length (mm) on suture age.

Squares, canine aged animals. Solid triangles, known-age animals (animals tagged as pups). __ __ __ = von Bertalanffy growth model; _ _ _ _ = Gompertz growth model; — = Logistic growth model.

DISCUSSION

Suture closure

Examination of suture age relative to SBL supported the sequence of FSC derived from chronological age, and suggested that: (i) full closure of the interparietal occurs before full closure of the coronal, and (ii) full closure of the maxillary occurs after full closure of the squamosal-jugal in some animals, i.e., basioccipito-basisphenoid, occipito-parietal, interparietal, coronal, squamosal-jugal and finally the maxillary.

With the exception of the squamosal-parietal, the sutures of the brain case (basioccipito-basisphenoid, occipito-parietal, coronal, interparietal) close before those of the face (squamosal-jugal; premaxillary-maxilla) (present study). As with other mammals, the brain case attains full size early in development (neural growth pattern) because early maturation of the brain case is essential for nervous control of the body (Moore, 1981).

The sequence of FSC reported by Rand (1949) based on male Cape fur seals of unknown chronological age was: basioccipito-basisphenoid, occipito-parietal, interparietal, coronal, squamosal-parietal, premaxillary-maxillary; interfrontal and basisphenoid-presphenoid (fully mature bulls, SBL *c.* 217 cm); and finally the internasal (i.e., old emaciated animals, SBL *c.* 223 cm). The maxillary was not examined. The sequence of FSC for the first 4 sutures was supported by the present study, and confirmed that certain sutures do not fully fuse until the animal is > 12 y (e.g., premaxillary-maxilla, maxillary, inter-frontal, basisphenoid-presphenoid and internasal).

In male *Zalophus californianus*, California sea lion, the sequence of PSC and FSC (n = 9 sutures) differed slightly from *A. p. pusillus*. The sequence of PSC was: basioccipito-basisphenoid, coronal/squamosal-parietal, occipito-parietal, interfrontal, interparietal, premaxillary-maxilla, basisphenoid-presphenoid and finally the maxillary, while the sequence of FSC was: basioccipito-basisphenoid, occipito-parietal, interparietal, squamosal-parietal, coronal, basisphenoid-presphenoid and finally the interfrontal/premaxillary-maxilla/maxillary, with all sutures fully closed by 15 y (n = 35 males, 1–15 y) (Orr & Schonewald, 1970).

In male *Callorhinus ursinus*, northern fur seal, the age at which the sutures begin to close and the length of time taken for sutures to fully close was slightly different than in *A. p. pusillus* (Scheffer & Wilke, 1953, present study). For example, the basioccipito-basisphenoid closes between 2 and 6 y; the occipito-parietal closes between 2 and 6 y; and the interparietal closes between 4 and 7 y (n = 121 males *C. ursinus*, 1–7 y). Other sutures were not examined.

Differences in growth rates/patterns, considerable individual variation between animals of similar age, and small sample size, would account for observed discrepancies within and between species.

Suture age as an indicator of chronological age

In male Cape fur seals, suture age can not be used as a reliable technique for estimating chronological age (present study).This is in agreement with comprehensive studies on humans (McKern, 1970; McKern & Stewart, 1957).

However, one of the sutures, the basioccipito-basisphenoid located at the base of the brain case, can be used independently as a ‘very rough’ indicator of age in male Cape fur seals (present study). The sequence of closure of the basioccipito-basisphenoid suture in Cape fur seals exhibited little variability, with complete fusion evident at 3 or 4 y. Examination of this suture reveals the following: (i) suture open = male ≤ 3 y old; (ii) suture fully closed = male 3–4 y or older and male has reached puberty[2].

Asymptotic size

As with other polygynous breeding pinnipeds which exhibit pronounce size dimorphism, full reproductive status (social maturity) is deferred until full size and competitive vigour are developed (Bartholomew, 1970; McLaren, 1993). Male Cape fur seals attain social maturity at 8–10 y (Stewardson *et al.*, 200X*a*). Although some males may grow to 220 cm, or more (Rand 1949), asymptotic size is estimated to be between 200 and 215 cm (present study).

Information on asymptotic size (Table 6.5) is advantageous for comparison among different species of pinnipeds because average size (including average adult size) may be more influenced by sampling biases, e.g., larger or smaller individuals may be over-represented in certain year/suture classes (McLaren, 1993). In the absence of an accurate method to determine the age of Cape fur seals > 13 y, asymptotic size estimated from suture age appears to be of practical value. Asymptotic size estimates derived from suture age and chronological age were found to be very similar, e.g., bacular length and mandibular length.

CONCLUSIONS

In this study we have demonstrated that in male Cape fur seals: (i) the sequence of PSC is different to the sequence of FSC; (ii) the age at which the sutures begin to close is different; (iii) the length of time taken for sutures to fully close is different; (iv) the sequence of FSC is basioccipito-basisphenoid, occipito-parietal, interparietal/coronal and finally the squamosal-jugal in males ≤ 12 y; (v) suture age is

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[2] Male Cape fur seals reach puberty at 3 or 4 y (Stewardson *et al.*, 1998).

not a reliable indicator of chronological age; and (vi) the basioccipito-basisphenoid can be used independently as an indicator of age. Furthermore, we have estimated asymptotic size for 10 morphological measurements inferred from suture age, a useful statistic for future comparative studies.

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STEWARDSON CL, PRVAN T, MEŸER MA (200X*b*) Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part two, skull. *Journal of Anatomy* (*Cambridge*) (submitted 2001).

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PART 3

GENERAL BIOLOGY

SEXUAL DIMORPHISM

CHAPTER 7

Sexual dimorphism in the adult Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): standard body length and skull morphology

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Manuscript submitted 2001.

ABSTRACT

We examine differences in body size and skull morphology ($n = 31$ variables) of male and female Cape fur seals, *Arctocephalus pusillus pusillus* ($n = 55$), from the coast of southern Africa. Males were found to be significantly larger than females in standard body length, with K-means cluster analysis successfully identifying 2 relatively homogeneous groups. Principal component analysis (covariance matrix) showed that the underlying data structure for male and female skull variables was different, and that most of this variation was expressed in overall skull size rather than shape. Males were significantly larger than females in 30 of the 31 skull variables. Breadth of brain case was the same for the genders. Relative to condylobasal length, males were significantly larger than females in 13 of the 30 skull variables. These were gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth, mastoid breadth, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid and height of mandible at meatus. In males, these variables were associated with the acquisition and defence of territory (e.g., large head size and mass; increased structural strength of the skull; increased bite capacity). Females were found to be significantly larger than males, relative to condylobasal length, with respect to breadth of brain case and length of upper postcanine row.

Key words: Pinnipeds, Otariidae, polygyny, sexual dimorphism, skull morphometrics, standard body length

INTRODUCTION

Sexual dimorphism is a form of non-geographic variation that can be generated in a species by the process of sexual selection (Schnell, Douglas & Hough, 1995). Highly polygynous species such as fur seals, sea lions, elephant seals, red deer and terrestrial monkeys, generally exhibit a high degree of sexual dimorphism (Schultz, 1969; Ralls, 1977; Clutton-Brock *et al.*, 1982). Differences in reproductive success among males of the species are large, and competition for access to females intense. Therefore, selection pressure appears to favour the development of traits that enhance male fighting ability, including body size, weaponry and skin thickness (Bartholomew, 1970; Selander, 1972; Le Boeuf, 1974; Hausfater, 1975, Alexander *et al.*, 1979; McCann, 1981; Clutton-Brock *et al.*, 1982).

Southern fur seals (*Arctocephalus* spp.) are among the most territorial of animals (Bonner, 1981). They are gregarious, polygynous and sexually dimorphic in body size. Male fur seals generally arrive at the rookeries around November to establish territories. Pregnant females arrive soon after. Once females are present in the male's territory, males guard females until they come into oestrus post-partum. Territorial size varies depending on the extent of competition. Females give birth within 1 week of coming ashore and then mate with the nearest male during the short breeding (pupping/mating) season. Males seldom leave the territory until the breeding season is over (Bonner, 1981). After mating, the territorial system gradually breaks down and males return to sea to replenish their physiological reserves. Males do not care for their young.

When establishing territories, male fur seals threaten each other with stereotyped vocal and visual displays (Bonner, 1968; Stirling, 1970; Miller, 1974). Fights may develop, occasionally resulting in severe injury or death (Rand, 1967; Trillmich, 1984; Campagna & Le Boeuf, 1988). In combat, fur seals usually bite their opponent; jerking or twisting upwards, ripping with their lower canines. In the larger species of fur seals, combat is usually a 'chest to chest pushing contest', with opponents gripping at each other's neck or foreflippers in an attempt to gain positional advantages (Rand, 1967: Miller, 1991).

Adult male fur seals are claimed to be about 3 times heavier and 1/3rd longer than adult females (Stirling, 1983; Boness, 1991). Large body size is advantageous in competitive interactions and enables breeding bulls to remain resident on territory for long periods of time without feeding (Rand, 1967; Miller, 1975; Payne, 1979; Stirling, 1983). Large males have a greater chance of holding territory, hence a greater opportunity to mate with more females. Strong forequarters, enlarged jaw and neck muscles, robust canines, increased structural strength of the skull, and long, thick neck hair (protective mane/wig), also appear to be potentially advantageous in the acquisition and maintenance of territory; quantitative information on these features, however, is lacking (Miller, 1991).

Here we examine morphological differences between skulls (n = 31 variables) of male and female Cape fur seals *Arctocephalus pusillus pusillus* (n = 55 animals), from the coast of southern Africa. Sexual dimorphism in body size is also investigated.

MATERIALS AND METHODS

Collection of specimens

Male Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34˚ 03'S, 23˚ 24'E) and East London (33˚ 03'S, 27˚ 54'E), from August 1978 to December 1995 (Stewardson *et al.*, 200Y*a*), and accessioned at the Port Elizabeth Museum (PEM). Routine necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). From this collection, skulls from 44 adults were selected for examination. Animals were aged from incremental lines observed in the dentine of upper canines (Stewardson *et al.*, 200Y*b*).

The sample was supplemented with measurements from 11 known-aged adults (animals tagged as pups) from Marine and Coastal Management (MCM), Cape Town.

Of the 55 animals examined in this study, 37 were adult males and 18 were adult females. All animals had reached full reproductive capacity, i.e., males ≥ 8 y (Stewardson *et al.*, 200Y*a*, 200Y*b*; Stewardson & Prvan, 200X) and females ≥ 3 y (J.H.M. David, pers. comm.). When age was not known, males ≥ 170 cm (Stewardson *et al.*, 200Y*b*) and females ≥ 135 cm (J.H.M. David, pers. comm.) were used in analysis. Animals > 13 y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes which terminates tooth growth. Estimated longevity is *c.* 20 y.

Skull variables

A total of 32 skull measurements was recorded (Table 7.1). However, 1 of these variables, height of sagittal crest, was not examined statistically because there were few measurements for females. Thus, statistical analysis was conducted on 31 of the 32 variables. Skull preparation and measurement procedures follow Stewardson *et al.*, (200Y*a*).

Statistical analyses

Four methods of analyses were employed. Firstly, the two sample t-tests (assuming equal variance) were used to test the hypothesis that the mean value of a skull variable was the same for males and females against an appropriate alternative hypothesis (H_0: $\mu_{males} = \mu_{females}$; H_1: $\mu_{males} > \mu_{females}$; H_1: $\mu_{females} > \mu_{males}$). Since more than 1 skull variable were being considered, the Bonferroni correction was used – the experimentwise error rate was divided by the total number of tests performed.

Secondly, K-means, a non-hierarchical cluster analysis, was used to classify each variable into 1 of 2 groups. Variables from both sexes were pooled so that initially the 2 groups (male and female) were unknown. Clustering was based on the 'similarity' of each variable. All variables were standardised and assigned to the cluster whose centroid (mean) was 'closest' using Euclidean distance (Johnson & Wichern, 1992).

Thirdly, plots of $\log_e$ of each skull variable against $\log_e$ of standard body length (SBL) for the genders were examined. 'Robust' regression (Huber M-Regression) was used to fit straight lines ($\log y = \log a + b \log x$) to the transformed data.

Finally, principal component analysis (PCA) was used. PCA is useful in identifying the most important sources of variation in anatomical measurements for various species (Jolliffe, 1986). Usually the first PC has all positive coefficients and according to Jolliffe (1986) this reflects overall 'size' of the individuals. The other PCs usually contrast some measurements with others and according to Jolliffe (1986) this can often be interpreted as reflecting certain aspects of 'shape' which are important to the species.

Skull measurements were recorded in the same units therefore a covariance matrix was used to calculate PCs (however this gives weight to larger, and hence possibly more variable measurements because the variables are not all treated on equal footing). Genders were examined separately because the grouped PCA was quite different in most cases to either the separate male PCA or female PCA.

PCA and two sample t-tests were calculated in Minitab (Minitab Inc., State College, 1999, 12.23). K-means cluster analyses[1] for skull variables and SBL were calculated in Minitab (Minitab Inc., State College, 1999, 12.23) and in SPSS (SPSS Inc., Chicago, Illinois, 1989–1999, 9.0.1), respectively. The regressions were fitted in S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

RESULTS

Standard body length

For available values, standard body length ranged from 157–201 cm in males ($n = 33$[2]) and 135–179 cm in females ($n = 18$). Mean lengths were 182.9 ± 2.3 and 149.1 ± 2.5, respectively. The two sample t-tests indicated that adult males were significantly larger than adult females (Table 7.1). The ratio of mean female SBL to mean male SBL was 1 : 1.23.

K-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 7.2). Of the 18 females, 17 (94%) were correctly classified. Of the 33 males, 28 (85%) were correctly classified.

Skull variables

Absolute skull size: two sample t-tests

The two sample t-tests indicated that 30 of the 31 mean skull variables were significantly larger in males than in females, i.e., we accept H_1: $\mu_{male} > \mu_{female}$ (Table 7.1, Fig. 7.1). Mean value of breadth of brain case was the same for the genders (Table 7.1).

The coefficient of variation was larger in males, with the following exceptions: least interorbital constriction, breadth of brain case, gnathion to anterior of foramen infraorbital and length of mandibular tooth row (Table 7.1).

Height of sagittal crest was not examined statistically, but was generally larger in most adult males.

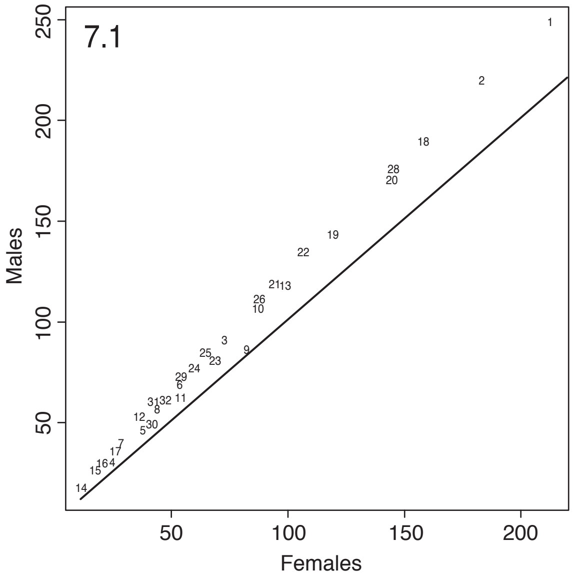

Fig. 7.1 Mean values of 31 skull variables for male and female Cape fur seals.

Numbers correspond to skull variables listed in Table 7.1. Numbers above the line, males > females; numbers on the line, males = females; numbers below the line, females > males.

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[1] Minitab could only perform K-means cluster analysis if there was ≥ 2 variables, therefore SBL (a single variable) was analysed in SPSS.

[2] SBL was not recorded for 4 of the 37 males (i.e., $n = 33$)

Table 7.1 ***Summary statistics (mean, S.E, C.V.) for skull measurements (mm) and standard body lengths (cm) from male and female Cape fur seals, and comparison between the mean of the two sexes (two sample t-test).*** Skull measurements relative to condylobasal length are given in brackets.

Skull variables	**Male**				**Female**				**Two sample t-test**			**Size**
	mean	**S.E.**	**C.V.**	***n***	**mean**	**S.E.**	**C.V.**	***n***	**T**	**P**	**DF**	**difference**
Dorsal												
D1 Condylobasal length	247.1	2.1	5.2	37	212.2	1.8	3.5	18	12.7	0.000	50	**M > F****
D2 Gnathion to middle of occipital crest	217.7 (0.88)	2.8 (0.005)	7.6 (3.43)	35	182.9 (0.86)	1.4 (0.004)	3.2 (2.07)	18	^{T}11.5 (2.64)	0.000 (0.011)	50 (49)	**M > F**** (M = F)
D3 Gnathion to posterior end of nasals	88.9 (0.36)	1.2 (0.003)	8.4 (4.72)	36	72.5 (0.34)	1.0 (0.003)	5.8 (4.26)	18	10.3 (3.96)	0.000 (0.000)	51 (39)	**M > F**** **(M > F**)**
D4 Greatest width of anterior nares	28.6 (0.12)	0.5 (0.001)	9.4 (6.98)	36	24.0 (0.11)	0.5 (0.002)	7.8 (6.87)	15	6.9 (0.96)	0.000 (0.345)	37 (27)	**M > F**** (M = F)
D5 Greatest length of nasals	44.0 (0.18)	0.9 (0.003)	11.7 (8.70)	35	37.5 (0.18)	0.7 (0.003)	7.4 (6.29)	17	5.9 (0.03)	0.000 (0.978)	49 (42)	**M > F**** (M = F)
D6 Breadth at preorbital processes	68.1 (0.28)	0.9 (0.002)	7.4 (4.61)	33	53.3 (0.25)	1.0 (0.003)	6.9 (5.15)	14	^{T}11.2 (5.95)	0.000 (0.000)	33 (24)	**M > F**** **(M > F**)**
D7 Least interorbital constriction	37.7 (0.15)	0.5 (0.002)	7.8 (7.12)	32	28.0 (0.13)	0.9 (0.003)	12.4 (10.45)	16	^{T}9.7 (5.52)	0.000 (0.000)	26 (24)	**M > F**** **(M > F**)**
D8 Breadth at supraorbital processes	56.8 (0.23)	0.9 (0.003)	9.3 (8.35)	33	43.9 (0.21)	1.0 (0.004)	8.9 (7.75)	16	9.6 (4.60)	0.000 (0.000)	38 (35)	**M > F**** **(M > F**)**
D9 Breadth of brain case	84.2 (0.34)	0.6 (0.003)	4.5 (5.63)	36	82.0 (0.39)	1.1 (0.005)	5.5 (5.09)	18	1.8 (7.87)	0.089 (0.000)	29 (33)	M = F **(F > M**)**
Palatal												
P10 Palatal notch to incisors	105.0 (0.42)	1.4 (0.004)	8.1 (5.12)	37	88.0 (0.41)	1.6 (0.007)	7.9 (6.75)	18	7.9 (1.30)	0.000 (0.204)	40 (27)	**M > F**** (M = F)
P11 Length of upper postcanine row	60.4 (0.24)	0.7 (0.002)	7.4 (6.08)	37	54.9 (0.26)	0.6 (0.003)	4.7 (4.58)	18	5.8 (3.87)	0.000 (0.000)	51 (41)	**M > F**** **(F > M**)**
P12 Greatest bicanine breadth	50.9 (0.21)	0.9 (0.002)	10.1 (6.75)	37	37.0 (0.17)	0.8 (0.003)	9.5 (6.80)	18	11.7 (8.72)	0.000 (0.000)	47 (39)	**M > F**** **(M > F**)**
P13 Gnathion to posterior end of maxilla	116.4 (0.47)	1.2 (0.002)	6.4 (2.82)	36	99.0 (0.47)	0.9 (0.002)	3.8 (1.71)	17	11.4 (1.83)	0.000 (0.740)	50 (47)	**M > F**** (M = F)
P14 Breadth of zygomatic root of maxilla	15.7 (0.06)	0.3 (0.001)	13.3 (10.19)	37	12.2 (0.06)	0.3 (0.001)	11.0 (10.27)	18	7.6 (3.49)	0.000 (0.001)	48 (36)	**M > F**** (M = F)
P15 Breadth of palate at postcanine 1	25.7 (0.10)	0.6 (0.002)	13.4 (11.05)	33	18.7 (0.09)	0.5 (0.002)	12.3 (10.39)	18	8.7 (5.32)	0.000 (0.000)	46 (42)	**M > F**** **(M > F**)**
P16 Breadth of palate at postcanine 3	27.8 (0.11)	0.5 (0.002)	10.9 (8.74)	34	21.1 (0.10)	0.3 (0.002)	6.7 (6.45)	17	10.8 (5.37)	0.000 (0.000)	48 (45)	**M > F**** **(M > F**)**
P17 Breadth of palate at postcanine 5	33.8 (0.14)	0.5 (0.002)	9.7 (7.71)	36	26.8 (0.13)	0.5 (0.002)	8.0 (8.02)	18	9.4 (3.42)	0.000 (0.002)	48 (35)	**M > F**** (M = F)
P18 Gnathion to hind border of postglenoid process	187.5 (0.76)	1.9 (0.002)	6.1 (1.56)	35	159.0 (0.75)	1.5 (0.003)	4.0 (1.43)	18	11.6 (2.43)	0.000 (0.020)	50 (37)	**M > F**** (M = F)
P19 Bizygomatic breadth	141.4 (0.57)	1.7 (0.006)	7.4 (5.88)	37	120.1 (0.57)	1.8 (0.005)	6.5 (4.10)	18	8.5 (0.87)	0.000 (0.388)	44 (46)	**M > F**** (M = F)

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Skull variables	**Male**				**Female**				**Two sample t-test**			**Size**
	mean	**S.E.**	**C.V.**	***n***	**mean**	**S.E.**	**C.V.**	***n***	**T**	**P**	**DF**	**difference**
Palatal												
P20 Basion to zygomatic root (anterior)	168.5 (0.68)	1.5 (0.002)	5.4 (1.70)	36	145.5 (0.69)	1.2 (0.003)	3.6 (1.62)	18	^{T}11.8 (1.61)	0.000 (0.117)	50 (35)	**M > F**** (M = F)
P21 Calvarial breadth	116.7 (0.47)	1.1 (0.003)	5.5 (3.20)	35	95.2 (0.45)	1.0 (0.003)	4.5 (2.79)	18	^{T} 14.4 (5.73)	0.000 (0.000)	50 (40)	**M > F**** **(M > F**)**
P22 Mastoid breadth	132.6 (0.54)	1.7 (0.004)	7.6 (4.26)	35	107.5 (0.51)	1.4 (0.005)	5.7 (3.80)	18	11.2 (5.13)	0.000 (0.000)	49 (40)	**M > F**** **(M > F**)**
P23 Basion to bend of pterygoid	79.0 (0.32)	0.6 (0.002)	4.5 (3.23)	35	69.4 (0.33)	0.7 (0.002)	4.1 (3.10)	18	10.6 (2.29)	0.000 (0.028)	41 (35)	**M > F**** (M = F)
Lateral												
L24 Gnathion to foramen infraorbital	75.0 (0.30)	0.9 (0.001)	7.0 (3.00)	37	60.8 (0.29)	1.1 (0.004)	7.3 (5.49)	17	10.3 (4.06)	0.000 (0.0006)	36 (21)	**M > F**** **(M > F*)**
L25 Gnathion to hind border of preorbital process	82.2 (0.33)	1.0 (0.002)	7.0 (2.87)	36	65.8 (0.31)	0.9 (0.003)	5.2 (3.36)	16	12.8 (6.77)	0.000 (0.000)	45 (26)	**M > F**** **(M > F*)**
L26 Height of skull at bottom of mastoid	108.7 (0.44)	1.8 (0.005)	10.0 (6.54)	36	88.7 (0.41)	1.5 (0.004)	5.7 (3.59)	11	8.5 (3.79)	0.000 (0.0006)	37 (33)	**M > F**** **(M > F**)**
L27[a] Height of sagittal crest	–	–	–	–	–	–	–	–	–	–	–	–
Mandibular												
M28 Length of mandible	173.7 (0.70)	1.7 (0.002)	5.9 (2.09)	36	146.2 (0.69)	1.9 (0.005)	5.5 (2.75)	17	10.6 (2.20)	0.000 (0.038)	39 (25)	**M > F**** (M = F)
M29 Length of mandibular tooth row	69.9 (0.29)	0.8 (0.002)	6.0 (4.49)	31	55.2 (0.26)	1.5 (0.007)	10.9 (11.19)	17	^{T}10.0 (^{T}3.70)	0.000 (0.001)	40 (26)	**M > F**** (M = F)
M30 Length of lower postcanine row	47.1 (0.19)	0.4 (0.001)	5.7 (4.55)	35	42.5 (0.20)	0.5 (0.002)	5.0 (4.47)	16	6.6 (3.62)	0.000 (0.001)	35 (28)	**M > F**** (M = F)
M31 Height of mandible at meatus	58.3 (0.24)	1.1 (0.003)	11.3 (7.97)	37	44.1 (0.21)	0.9 (0.003)	8.7 (6.64)	17	10.0 (6.10)	0.000 (0.000)	48 (41)	**M > F**** **(M > F**)**
M32 Angularis to coronoideus	58.7 (0.24)	1.0 (0.003)	10.5 (6.70)	35	47.3 (0.22)	0.9 (0.003)	7.4 (6.01)	17	8.4 (3.22)	0.000 (0.0026)	48 (37)	**M > F**** (M = F)
Standard body length	182.9	2.3	7.2	33	149.1	2.5	7.1	18	10.0	0.000	41	**(M > F**)**

[a] Height of sagittal crest (L27) was not examined statistically because there were few measurements for females. However, in large animals, males crest height was greater than female crest height.

^{T} Normality assumption did not hold (data skewed); therefore the data was transformed using Box-Cox transformation (Myers, 1990).

n, number of animals.

* Significant at the 5% level, with Bonferroni correction.

** Significant at the 1% level, with Bonferroni correction.

DF were calculated for a two sample t-test assuming unequal variance.

Refer to Stewardson *et al.*, (200Y*a*) for a full description of skull measurement procedures.

The canines were not measured, but were considerably broader in adult males.

Relative skull size: two sample t-tests

When skull variables were analysed relative to condylobasal length (CBL), males were found to be significantly larger than females for 13 (43%) variables: gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth, mastoid breadth, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid and height of mandible at meatus (Table 7.1, Fig. 7.2). Differences between the genders were highly significant, apart from gnathion to anterior of foramen infraorbital and height of skull at base of mastoid, which were significant at the 5% level (Table 7.1).

Breadth of brain case was the same in ‘absolute size’ for males and females, but ‘relative to CBL’ females were larger than males (Table 7.1). Length of upper postcanine row was larger in ‘absolute size’ in males, but ‘relative to CBL’ females were larger than males (Table 7.1).

The remaining 15 (50%) variables were equal for the genders (Table 7.1). Since males were larger than females in ‘absolute size’, this suggested that the 15 variables were proportionate to CBL regardless of sex, i.e., the ratio ‘relative to CBL’ was the same for the genders.

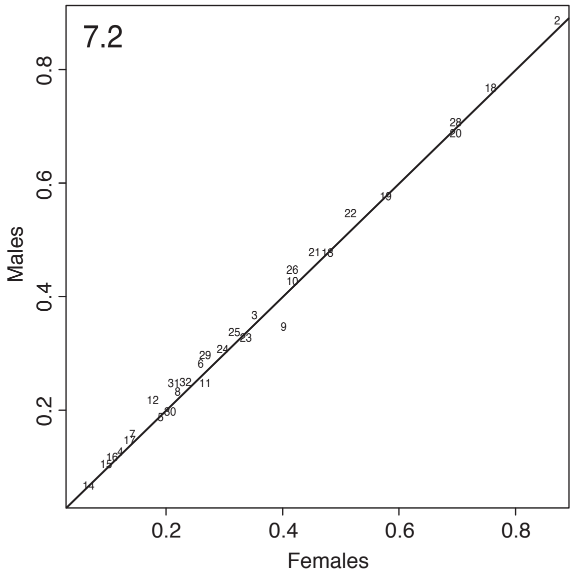


Fig. 7.2 Mean values of 30 skull variables, relative to condylobasal length, for male and female Cape fur seals.

Numbers correspond to skull variables listed in Table 7.1. Numbers above the line, males > females; numbers on the line, males = females; numbers below the line, females > males.

The coefficient of variation for values ‘relative to CBL’ was larger in males for about 1/3 rd of all variables (Table 7.1). Exceptions were breadth at preorbital processes, least interorbital constriction, palatal notch to incisors, breadth of zygomatic root of maxilla, breadth of palate at postcanine 5, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, length of mandible and length of mandibular tooth row. The coefficients of 2 of these variables (least interorbital constriction and length of mandibular tooth row) were considerably larger in females in both ‘absolute size’ and size ‘relative to CBL’.

K-means cluster analysis

K-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 7.2). Classification based on dorsal, palatal and mandibular observations was highly successful in recapturing the 2 groups. Classification based on lateral observations was less successful.

Apart from 1 mandibular variable, all females were correctly classified. The majority of males were correctly classified with the following exceptions – 1 dorsal, 2 palatal, 2 mandibular and 7 lateral variables were incorrectly classified as females (Table 7.2). Misclassification occurred in small males only.

Linear regression

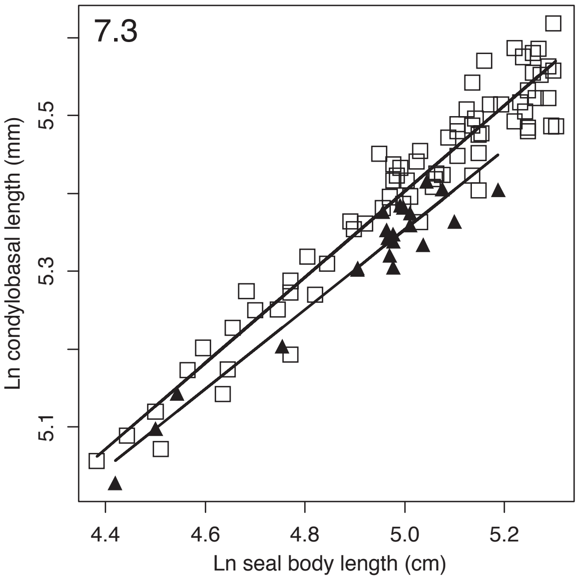
All transformed variables were regressed on $\log_e$ SBL. Three variables which best depicted maximum discrimination between the sexes, using regression, are given in Fig. 7.1–7.3. These were CBL, greatest

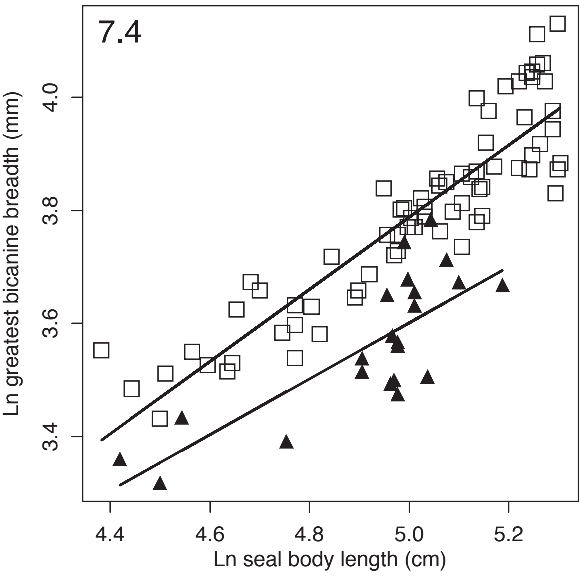
Table 7.2 ***Classification of skull measurements using K-means clusters analysis***

Skull variables	**Cluster 1**	**Cluster 2**	***n***
***Dorsal**			
male	22 (96%)	1 (4%)	23
female	0	11 (100%)	11
***Palatal**			
male	24 (92%)	2 (8%)	26
female	0	17 (100%)	17
***Lateral**			
male	28 (80%)	7 (20%)	35
female	0	10 (100%)	17
***Mandibular**			
male	25 (93%)	2 (7%)	27
female	1 (6%)	16 (94%)	17
Standard body length			
male	28 (85%)	5 (15%)	33
female	1 (6%)	17 (94%)	18

n, number of animals.

* Standardised variables.





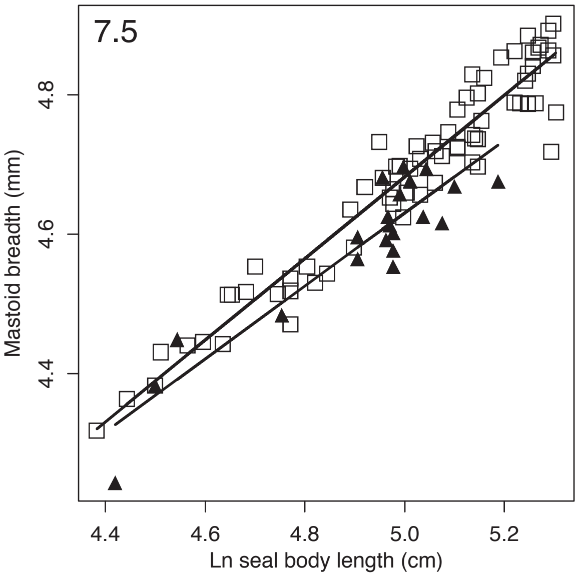


Fig. 7.3–7.5 Bivariate plot of: (3) log CBL (mm) on log SBL (cm); (4) log greatest bicanine breadth (mm) on log SBL (cm); (5) log mastoid breadth (mm) on log SBL (cm). Squares, males. Solid triangles, females.

bicanine breadth and mastoid breadth. These plots clearly show pronounce sexual dimorphism in adult Cape fur seals, supporting findings of the two sample t-test and K-means cluster analysis.

Principal component analysis

The first 3 PCs accounted for most of the variation. The first PC (PC1) can be interpreted as a measure of overall skull size while PC2 and PC3 define certain aspects of shape (Table 7.3). Interpretations for the first 3 PCs for the 2 genders are given in Table 7.4, together with the percentage of total variation given by each PC. The variances of corresponding PCs for the 2 genders do vary and interpretations are dissimilar for most pairs of PCs.

Can you determine the gender of an isolated skull without measuring it?

It is possible to visually determine the gender of an isolated Cape fur seal skull, provided the skull is from an adult animal. However, visual identification based on morphology of the skull alone can be misleading, e.g., young adult males can be mistaken for older females. Therefore, before examining the skull, it is advisable to age the specimen first (i.e., count the GLGs in the upper canine).

The skull of an adult male ≥ 10 y is larger (CBL ≥ 248 mm; mastoid breadth ≥ 134 mm) and more robust than the skull of a similar aged female. In males, the canines are considerably broader, and the sagittal/occipital crests are more pronounced (but variable in height). In adult males, bony deposits occur throughout the parietal region which become more prominent with increasing age (Stewardson *et al.*, 200Y*a*; present study, Rand, 1949*a*, *b*). Mean size of sexually dimorphic traits, according to age (y), have been summarised elsewhere (Stewardson *et al.*, 200Y*a*).

Table 7.3 ***Principal component analysis of covariance matrix for adult male and adult female Arctocephalus pusillus pusillus, showing principal components, eigenvalues, proportions and cumulative proportions of the first three principal components***

Skull variable	**PC I**	**PC II**	**PC III**	**PC I**	**PC II**	**PC III**
Dorsal		**Males (n = 23)**			**Females (n = 10)**	
D1 Condylobasal length	-0.58	-0.35	-0.50	-0.61	0.48	0.38
D2 Gnathion to middle of occipital crest	-0.71	-0.06	0.52	-0.28	-0.001	-0.32
D3 Gnathion to posterior end of nasals	-0.28	0.30	-0.28	-0.24	-0.49	0.09
D4 Greatest width of anterior nares	-0.10	0.16	0.03	-0.16	0.28	0.06
D5 Greatest length of nasals	-0.16	0.34	0.02	-0.08	-0.25	0.04
D6 Breadth at preorbital processes	-0.19	0.30	-0.28	-0.41	0.15	-0.17
D7 Least interorbital constriction	-0.08	0.29	0.09	-0.37	-0.15	-0.14
D8 Greatest breadth at supraorbital processes	-0.08	0.49	0.38	-0.36	-0.39	-0.43
D9 Breadth of brain case	-0.03	-0.48	0.41	-0.15	-0.44	0.71
Eigenvalue	***444.9***	***36.1***	***15.7***	***93.7***	***17.7***	***12.7***
Proportion	***0.84***	***0.07***	***0.03***	***0.68***	***0.13***	***0.09***
Cumulative	***0.84***	***0.91***	***0.94***	***0.68***	***0.81***	***0.91***
Palatal		**Males (n = 26)**			**Females (n = 16)**	
P10 Palatal notch to incisors	-0.31	-0.21	0.82	-0.34	0.83	0.32
P11 Length of upper postcanine row	-0.13	-0.13	0.10	-0.08	-0.06	-0.02
P12 Greatest bicanine breadth	-0.19	0.03	-0.01	-0.20	-0.08	-0.19
P13 Gnathion to posterior end of maxilla	-0.30	-0.34	-0.06	-0.24	0.04	0.10
P14 Breadth of zygomatic root of maxilla	-0.07	-0.01	-0.003	-0.03	-0.04	0.04
P15 Breadth of palate at postcanine 1	-0.10	0.03	-0.14	-0.11	0.08	-0.21
P16 Breadth of palate at postcanine 3	-0.08	0.04	-0.08	-0.03	0.09	-0.24
P17 Breadth of palate at postcanine 5	-0.10	0.05	-0.14	-0.02	0.08	-0.24
P18 Gnathion to posterior border of postglenoid process	-0.50	-0.18	-0.06	-0.41	-0.16	-0.21
P19 Bizygomatic breadth	-0.30	0.86	0.23	-0.53	-0.15	0.27
P20 Basion to zygomatic root	-0.41	-0.11	-0.13	-0.30	0.13	-0.66
P21 Calvarial breadth	-0.25	0.13	-0.31	-0.26	-0.15	0.19
P22 Mastoid breadth	-0.39	0.05	-0.28	-0.37	-0.42	0.17
P23 Basion to bend of pterygoid	-0.13	-0.08	-0.13	-0.13	0.14	0.26
Eigenvalue	***507.1***	***84.4***	***35.0***	***155.5***	***44.4***	***13.9***
Proportion	***0.73***	***0.12***	***0.05***	***0.62***	***0.18***	***0.06***
Cumulative	***0.73***	***0.85***	***0.90***	***0.62***	***0.79***	***0.85***
Lateral		**Males (n = 35)**			**Females (n = 10)**	
L24 Gnathion to anterior of foramen infraorbital	0.39	-0.56	0.73	0.24	-0.71	0.66
L25 Gnathion to posterior border of preorbital process	0.43	-0.59	-0.68	0.33	-0.58	-0.74
L26 Height of skull at base of mastoid	0.82	0.58	0.01	0.91	0.40	0.09
L27[a] Height of sagittal crest	–	–	–	–	–	–
Eigenvalue	***153.8***	***14.5***	***0.7***	***31.4***	***6.3***	***0.8***
Proportion	***0.91***	***0.09***	***0.004***	***0.82***	***0.16***	***0.02***
Cumulative	***0.91***	***0.996***	***1.00***	***0.82***	***0.98***	***1.00***
Mandibular		**Males (n = 26)**			**Females (n = 16)**	
M28 Length of mandible	-0.73	0.38	-0.41	-0.86	-0.20	-0.35
M29 Length of mandibular tooth row	-0.19	0.45	0.57	-0.13	0.96	-0.23
M30 Length of lower postcanine row	-0.12	0.47	0.13	-0.15	-0.09	-0.37
M31 Height of mandible at meatus	-0.49	-0.48	0.63	-0.37	0.05	0.50
M32 Angularis to coronoideus	-0.42	-0.46	-0.31	-0.30	0.14	0.66
Eigenvalue	***145.2***	***13.9***	***8.0***	***88.5***	***27.2***	***9.1***
Proportion	***0.84***	***0.08***	***0.05***	***0.70***	***0.21***	***0.07***
Cumulative	***0.84***	***0.92***	***0.97***	***0.70***	***0.91***	***0.98***

Proportion gives the amount of the total variation that the PC accounted for.
Cumulative gives the amount the first PC accounted for, then the amount that the first two PCs accounted for and finally the amount of total variation the first three PCs accounted for.

[a] Height of sagittal crest (L27) was not examined statistically because there were few measurements for females.

Table 7.4 *Interpretations for the first 3 principal components for adult male and adult female Arctocephalus pusillus pusillus*

Male	Female
Dorsal	
Component 1 (male 84%, female 68%)	
CBL and gnathion to middle of occipital crest measure overall size.	CBL, breadth at preorbital processes, least interorbital constriction and greatest breadth at supraorbital processes measures overall size.
Component 2 (male 7%, female 13%)	
Contrasts greatest breadth at supraorbital processes with CBL and breadth of brain case.	Contrasts CBL with gnathion to posterior end of nasals, greatest breadth at supraorbital processes and breadth of brain case.
Component 3 (male 3%, female 9%)	
Contrasts CBL with gnathion to middle of occipital crest, greatest breadth at supraorbital processes and breadth of brain case.	Contrasts greatest breadth at supraorbital processes with CBL and breadth of brain case.
Palatal	
Component 1 (male 73%, female 62%)	
Gnathion to posterior border of postglenoid process, basion to zygomatic root and mastoid breadth measure overall size.	Gnathion to posterior border of postglenoid process, bizygomatic breadth and mastoid breadth measure overall size.
Component 2 (male 12%, female 18%)	
Bizygomatic breadth dominates.	Contrasts palatal notch to incisors with mastoid breadth.
Component 3 (male 5%, female 6%)	
Palatal notch to incisors dominates.	Basion to zygomatic root dominates.
Lateral*	
Component 1 (male 91%, female 82%)	
Height of skull at base of mastoid, gnathion to posterior border of preorbital process and gnathion to anterior of foramen infraorbital measure overall size.	Height of skull at base of mastoid measures overall size
Component 2 (male 9%, female 16%)	
Contrasts height of skull at base of mastoid with gnathion to anterior of foramen infraorbital and gnathion to posterior border or preorbital process.	Contrasts height of skull at base of mastoid with gnathion to anterior of foramen infraorbital and gnathion to posterior border of preorbital process.
Mandibular	
Component 1 (male 84%, female 70%)	
Length of mandible, height of mandible at meatus and angularis to coronoideus measure overall size.	Length of mandible and height of mandible at meatus measure overall size.
Component 2 (male 8%, female 21%)	
Contrasts height of mandible at meatus and angularis to coronoideus with others (length of mandible, length of mandibular tooth row, length of lower postcanine row).	Length of mandibular tooth row dominates.
Component 3 (male 5%, female 7%)	
Contrasts length of mandible with length of mandibular tooth row and height of mandible at meatus.	Contrasts length of mandible and length of lower postcanine row with height of mandible at meatus and angularis to coronoideus.

Covariance matrix used.
Variables that contributed predominantly to size and/or shape are listed above, i.e., variables with loadings ≥ 0.36 (absolute value).
* Only 2 PCs considered.

DISCUSSION

Possible bias

Several factors must be taken into consideration when interpreting the data. Firstly, there may be an over representation of either larger or smaller individuals in the data set which may possibly bias the results. Secondly, although identical variables were taken from PEM and MCM animals, PEM variables were recorded by the first author whereas MCM variables were recorded by the third author, introducing possible inter-observer error.

Principal component analysis: skull size and shape

For both genders, CBL, mastoid breadth, height of skull at base of mastoid, gnathion to posterior border of postglenoid process and length of mandible contributed the most to overall skull size. Gnathion to middle of occipital crest and basion to zygomatic root were predominant in males but not in females. Bizygomatic breadth was predominant in females but not in males.

Predominant variables contributing to shape in both genders were CBL, breadth at supraorbital processes, breadth of brain case, palatal notch to incisors, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid, length of mandible, length of mandibular tooth row, length of lower postcanine row, height of mandible at meatus and angularis to coronoideus.

Bizygomatic breadth contributed predominantly to skull shape in males but not in females. Gnathion to posterior end of nasals, basion to zygomatic root and mastoid breadth contributed predominantly to skull shape in females but not in males.

These findings indicate that the underlying data structure for males and females was different. Differences occurred in the combination of predominant variables, and in their magnitude and sign.

General pattern of growth

Although male Cape fur seals are slightly heavier than females (4.5–6.4 kg) at birth, growth patterns for the genders are similar up until puberty. Males attain puberty between 3 and 4 y (Stewardson *et al.*, 1998) and females between 3 and 5 y (J.H.M David, pers. comm.).

Although males are sexually mature at an early age, they are physically unable to hold a harem until much latter. Full reproductive status (social maturity) is deferred until full size and competitive vigour are developed. Females approximate adult size at *c.* 5 y, while males approximate adult size between 8 and 10 y (Stewardson *et al.*, 200Y*b*; Stewardson & Prvan, 200X). Adult males may weigh up to 353 kg (mean, 250 kg), while females may weigh up to 122 kg (mean, 58 kg) (J.H.M David, pers. comm.). Similar growth patterns in body size have been reported in other polygynous breeding pinnipeds which exhibit pronounce size dimorphism, e.g., *Callorhinus ursinus*, northern fur seals (McLaren, 1993).

Development of the skull also differs between the genders, with male Cape fur seals exhibiting monophasic growth in some variables and biphasic growth in others, while females exhibit only monophasic growth (Stewardson *et al.*, 200Y*a*). In males, biphasic growth is associated with territorial acquisition and maintenance (Stewardson *et al.*, 200Y*a*). Similar growth patterns have been reported in the skulls of other southern fur seals, e.g., *A. p. doriferus*, Australian fur seal, and *A. forsteri*, New Zealand fur seal (Brunner, 1998).

Differences in growth patterns between the genders support our findings of pronounced sexual dimorphism in this species.

Variation among adult males

The coefficient of variation for most skull variables was larger in males than in females (present study). Variability in adult males at least partly reflects differences in social status. Considering that only a small percentage of males become breeding bulls, we suggest that secondary sexual characteristics may not fully develop in non-breeding males, of similar age, that do not hold territories. Differences in physical appearance will be most noticeable before and during the breeding season when breeding bulls build up their body reserves.

Loci of sexual dimorphism

Dorsal

Males were significantly larger than females ‘relative to CBL’ in 44% ($n = 4$) of dorsal variables (gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes). In both genders, these variables form part of the splanchnocranium (gnathion to posterior end of nasals) and the frontal region (least interorbital constriction and breadth at supraorbital processes), and are associated with respiration/vocalisation (gnathion to posterior end of nasals) and feeding (breadth at supraorbital processes).

In males, at least 2 of these variables have obvious functional significance with respect to territorial acquisition and defence. Least interorbital constriction and breadth at supraorbital processes contribute to the structural strength of the skull, and shield the animal against blows to the head (especially the eyes) during combat with rival males.

Palatal

Males were significantly larger than females ‘relative to CBL’ in 36% ($n = 5$) of palatal variables (greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth and mastoid breadth). In both genders, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, form part of the palatal region and are associated with feeding (greatest bicanine breadth, breadth of palate at postcanine 1 and 3) and respiration/vocalisation (greatest bicanine breadth). Calvarial breadth and mastoid breadth form part of the basicranium and are associated primarily with auditory function (calvarial breadth, mastoid breadth).

Enlargement of the canines (greatest bicanine breadth) enables males to inflict a potentially lethal bite during combat. The rostrum is broad (palatal breadth at postcanine 1 and 3), accommodating the large canines. Enlargement of calvarial breadth and mastoid breadth increases physical appearance and structural strength of the skull (large head size/mass).

Lateral

Males were significantly larger than females ‘relative to CBL’ in all lateral variables (gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid). In both genders, gnathion to anterior of foramen infraorbital and gnathion to posterior border of preorbital process form part of the splanchnocranium and are associated with respiration/ vocalisation.

Enlargement of skull height and facial length in males, increases overall head size. Large size is advantageous in territorial acquisition and maintenance.

Mandible

Males were significantly larger than females 'relative to CBL' in only 1 mandibular variable (height of mandible at meatus). This variable is associated with auditory function and feeding in both genders. Enlargement of this variable in males, increases gape and provides a larger surface area for muscle (masseter and temporalis) attachment. Large jaws and jaw muscles are advantageous in territorial combat.

Sexual dimorphism of the skull in southern fur seals has been reported for *A. p. doriferus* and *A. forsteri* (Brunner, 1998). As with the Cape fur seal, sexually dimorphic traits are mainly those characteristics that increase the ability of males to acquire and defend territory.

Significance of the dimorphism

In male Cape fur seals, their appears to be strong selection pressure for the development of certain morphological traits associated with fighting ability. Development of these traits is not evident in female Cape fur seals, hence dimorphism between the genders.

Firstly, in male Cape fur seals, selection pressure appears to favour large body size. For the range of available values in this study, males (mean, 183 cm) were shown to be significantly larger in standard body length than females (mean, 149 cm). Large males in breeding condition may be 4–5 times heavier than adult females (David, 1989). These large males have an advantage over their smaller rivals in gaining high social rank through fighting. Furthermore, large males in breeding condition have a well developed fat store. This thick blubber layer enables males to remain resident on territory for long periods (up to 40 days) without feeding. If a male abandons his territory to feed, this may result in a rival male mating with his females and/or increase the risk of injury when re-claiming his territory, thus decrease his opportunity of multiple matings.

Secondly, selection pressure appears to favour the development of certain skull traits that appear to be associated with fighting ability. In the present study, traits which are significantly larger in males appear to be associated with bite force (e.g., broad canines, increased surface area for muscle attachment, large gape), large head size/mass (e.g., increased mastoid and calvarial breadth) and/or structural strength of the skull (shields against direct blows to the head during combat).

As with other male fur seals, selection pressure favours traits associated with fighting ability because the length of time a male can hold territory among breeding females is critical to his genetic success (Bartholomew, 1970). Large body size and the development of weaponry would increase social rank in this polygynous breeding species, hence, increase the opportunity of multiple matings. Large, dominant male Cape fur seals may mate with 10–30 adult females during the short (6–8 weeks) breeding season.

CONCLUSIONS

Information presented in the study demonstrates that there is pronounced sexual dimorphism in adult Cape fur seals with respect to body size, skull size and skull shape. Male Cape fur seals were significantly larger than females in SBL, and 43% of skull variables were found to be significantly larger in males 'relative to CBL'. These variables were associated with fighting ability, e.g., large head size/mass, increased structural strength of the skull and/or increased bite capacity. Principal component analysis showed that the underlying data structure for males and females was different, and that most variation between the sexes was expressed in overall skull size rather than shape. Condylobasal length, height of skull at base of mastoid and length of mandible contributed considerably to overall size, with gnathion to middle of occipital crest predominating in males only.

Further studies are required to test the suggestion that secondary sexual characteristics may not fully develop in non-breeding males that do not hold territories.

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PART 4

GENERAL BIOLOGY

REPRODUCTION

CHAPTER 8

Reproduction in the male Cape fur seal *Arctocephalus pusillus pusillus:* age at puberty and annual cycle of the testis

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ABSTRACT

Seasonal changes in the reproductive anatomy and histology of the male Cape fur seal *Arctocephalus pusillus pusillus* were examined. Studies were based on 99 specimens collected between Algoa Bay on the south-east coast of South Africa, and Cape Frio, Namibia, during 1974 to 1990. Reproductive organs are briefly described. The presence of sperm in the seminiferous and epididymal tubules indicates that males attain puberty between 3 and 4 years of age. Quantitative measurements of testis weight, testis volume and the diameter of the seminiferous and epididymal tubules were analysed on a monthly basis and spermatogenesis documented. Although some males may remain in breeding condition until March, the absence of spermatozoa in the epididymis during February to June, when mean testis mass and mean tubule diameter reached a minimum, clearly showed reproductive quiescence following the rut. Four stages of spermatogenesis were observed: (1) inactive (February/March–June); (2) early spermatogenesis (July); (3) late spermatogenesis (July/August–December/January); and (4) epithelial regression (February–June). Individual variation between males, possibly differences in social status and body condition, may influence the duration of spermatogenesis, hence the overlap in duration between epithelial regression and inactivity. It appears that photoperiod may act as an obligatory proximate factor initiating spermatogenesis 3–4 months before the relatively short breeding season from November to December.

Key words: Cape fur seal, *Arctocephalus pusillus pusillus*, reproduction, testis, histology, spermatogenesis, annual cycle

INTRODUCTION

Following some earlier anatomical studies reviewed by Harrison (1969) and Laws & Sinha (1993), there has been little concerted effort to document the seasonal cycle or physiology of reproduction in male pinnipeds (Boyd, 1991). Detailed anatomical and histological descriptions of the annual cycle of the gonads (Laws, 1956; Griffiths, 1984*a*, *b*), age at puberty (Laws, 1956), and endocrine regulation of seasonal breeding (Griffiths & Bryden, 1981; Griffiths, 1985) have been compiled for the southern elephant seal *Mirounga leonina*. Other pinniped species have been less well studied (Boyd, 1991; Laws & Sinha, 1993). With the exception of the sub-Antarctic fur seal *Arctocephalus tropicalis* (Bester, 1990) and the northern fur seal *Callorhinus ursinus* (Kenyon *et al.,* 1954; Ashchepkova & Fedoseev, 1988), our understanding of the seasonal cycle of reproduction in male otariids is rudimentary.

It is thought that males of all seasonally breeding pinnipeds experience periods of fertility and infertility (Boyd, 1991). However, difficulties in obtaining reproductive material outside the breeding season have generally restricted longitudinal seasonal studies that might confirm this theory (see Hamilton, 1939; Bertram, 1940; Harrison *et al.,* 1952; Harrison, 1960; Bigg, 1969). Seasonal breeding, in which periods of sexual quiescence alternate with periods of sexual activity, has been documented in several species of phocids (Laws, 1956; McLaren, 1958; Carrick, Csordas & Ingham, 1962, Carrick, Csordas, Ingham & Keith, 1962, Boulva & McLaren, 1979; Griffiths, 1984*a*, *b*; Ryg, Smith & Oritsland, 1991), and two species of otariids – *C. ursinus* (Kenyon *et al.*, 1954; Ashchepkova & Fedoseev, 1988) and *A. tropicalis* (Bester, 1990). Preliminary findings suggest that the gonads of the Antarctic fur seal *Arctocephalus gazella* are also seasonally active (Laws & Sinha, 1993). These studies indicate that mean testis mass and seminiferous tubule diameter increase before and during the breeding season. The testes then regress and the epididymis is aspermatic. Testicular changes coincide with the onset and cessation of spermatogenesis.

The present paper provides a monthly description of the annual cycle of the testis and epididymis in the male Cape fur seal *Arctocephalus pusillus pusillus* with quantitative measurements of testis weight, testis volume, and the diameter of the seminiferous and epididymal tubules. A photographic record of the spermatogenic cycle is presented and age at puberty determined. A brief description of reproductive anatomy in an 8-year old male is also provided.

Study animal

Arctocephalus p. pusillus breeds at 25 colonies distributed from Algoa Bay (lat. 34˚S, long. 26˚E) on the south-east coast of South Africa, to Cape Cross (lat. 21˚46'S, long. 13˚57'E), Namibia. Preferred habitat and associated climatic conditions have been described by Rand (1967) and Warneke & Shaughnessy (1985). As with other otariids, annual reproduction is characterized by synchronous breeding, embryonic diapause, a polygynous breeding system, pronounced sexual dimorphism, copulation soon after parturition, protracted lactation periods and, a comparatively slow pup growth rate. The breeding (pupping and mating) season extends from November to late December (Shaughnessy & Best, unpubl. report). Reproduction in the female has been described (Rand, 1955; Warneke & Shaughnessy, 1985; David & Rand, 1986); however, little is known of the male cycle.

MATERIALS AND METHODS

Cape fur seals were collected at random during Sea Fisheries Research Institute research cruises and routine field trips to breeding rookeries between 34˚S, 26˚E and 18˚S, 12˚E from 1974 to 1990. Most animals were shot at sea with a 12-bore shotgun for dietary studies; collection details are provided by David (1987*a*).

In the field, routine necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). The right testis with attached epididymis was measured (length × width × height) to the nearest 1.0 mm, frozen, and brought back to the laboratory to be weighed on an electronic balance. An equatorial segment of each left testis with attached epididymis was stored in 10% phosphate buffered formalin for subsequent histological analysis. Upper canines were collected for age determination. Specimens were accessioned at the Sea Fisheries Research Institute, Cape Town. From this collection, 99 males – 10 months to 13^+ years of age – were selected for reproductive studies: 40 males (< 5 years) were examined to determine age at puberty and 59 males (≥ 4 years of age) were used to determine the yearly cycle of the testis and epididymis.

The gonads of males < 5 years of age ($n = 40$ seals) were examined to determine the age at puberty; the age at which sperm first accumulates within the seminiferous and epididymal tubules in quantity. These animals were collected during September to January when pubertal males should be in reproductive condition (see Results). Testes were considered pre-pubertal when the tubules were completely aspermatic and the epididymis was devoid of sperm. All males < 4 years of age ($n = 21$) had been tagged within 6 weeks of birth and were therefore of known-age.

The gonads of post-pubertal males ≥ 4 years of age ($n = 59$ seals) were examined to determine the annual cycle of the testis and epididymis (i.e., 4–5 seals for each calendar month). Preliminary age determination suggested males 4 years of age were at least 145 cm long (SBL); therefore, seals exceeding this length were selected from the collection and then aged at a later date. Seasonal studies were limited to 4–5 adult males per month because few specimens were collected during the summer period and accessioned material was not always suitable. Although socially mature specimens were included in this study, territorial status was unknown because animals were shot at sea. Males in prime 'breeding condition' were not collected from territories.

The body of the left testis, and the attached epididymis of each specimen were sliced into thin cross-sections, dehydrated, and embedded in paraplast-wax using standard histological procedures (Drury & Wallington, 1967). Equatorial segments were sectioned at 5 µm and stained with Ehrlich's haematoxylin and counter-stained in eosin. An image analysing computer (Quantimet 520, Cambridge Instruments) was used to measure the diameter of both the seminiferous and epididymal tubules. Specimens (n = 59) were examined under × 10 objective and diameters were calculated as the mean of 10 measurements of circular profile. The nucleus diameter of 20 randomly selected Leydig cells from 4 males collected in June (gonads inactive) and 4 males collected during August (gonads active) were measured to 0.5 µm using an eyepiece micrometer.

Histological sections of the testis and epididymis were categorized into one of 4 stages: (1) inactive (spermatogonia and Sertoli cells present; no sperm in the epididymis); (2) early spermatogenesis (spermatogonia and spermatocytes present; no sperm in the epididymis); (3) late spermatogenesis (spermatogonia, spermatocytes, spermatids and spermatozoa present; sperm in epididymis) and (4) epithelial regression (reduced number of epithelial cells with evidence of degeneration; sperm absent from the epididymis). Specimens were assigned to a given category if > 50% of the tubules examined (i.e., 50 seminiferous/10 epididymal tubules per animal) showed features characteristic of that condition (modified from Bernard, Cotterill & Fergusson, 1996).

An additional tissue processing technique was incorporated into this study in order to document the finer detail of the spermatogenic cycle. The left testis was sliced into 8 × 2 mm sections and rinsed 3 times in 0.075 M sodium phosphate. Tissues were dehydrated in 70% ethanol (15 min), 100% ethanol (15 min), 100% n-propanol (1 h) and 100% n-butanol (1 day). Dehydrated tissues were placed in gelatin capsules filled with complete monomer solution (dissolve 180 ml purified glycol methacrylate; 12 ml PEG/Carbowax 200^{T} and 1 g benzoyl peroxide using an ultra sound) and infiltrated at room temperature for 12 h, 12 h, and then 3 days, following changes in solution. Tissues were then placed in an oven (24 h at 60˚C) for polymerization, sectioned at 2 µm using an ultra-microtome and stained with 0.5% toluidine blue borax buffer for light microscopical observations (modified from Feder & O'Brien, 1968).

The age of animals was estimated from counts of incremental lines observed in the dentine of tooth sections. Upper canines were sectioned longitudinally using a circular diamond saw. Sections were ground down to 280–320 µm, dehydrated, embedded in resin and viewed under a stereomicroscope in polarized light (Oosthuizen, 1997). Each section was counted 5 times by an individual reader and ages were rounded off to the nearest birth date. The median date of birth was assumed to be 1 December (Shaughnessy & Best, unpubl. report). Closure of the pulp cavity prevented precise age determination of older animals (i.e., > 13 years) (Oosthuizen, 1997).

Mean testis volume was calculated as follows: (testis width + testis height)/2) × π × testis length (Graham Ross, pers. comm.). Monthly and seasonal reproductive parameters were compared using 1-way analysis of variance (ANOVA), Genstat 5 Release 3 (Genstat 5 Committee, 1993). Mean values are given as ± 1 standard deviation unless otherwise stated.

RESULTS

Morphology

The otariid testes are said to be scrotal (Laws & Sinha, 1993). In the adult male Cape fur seal, the scrotum appears to be fully pendulous only when the animal is in prime 'breeding condition', actively defending territory. However, for animals shot at sea and not actively defending territory, the testes are usually withdrawn into the groin, positioned obliquely either side of the penis, external to the muscle of the abdominal wall (Fig. 8.1). The left testis is more caudal than the right. The testis and epididymis are enclosed in the tunica albuginea. The epididymis is a narrow, elongated structure (with little differentiation into caput, cauda and corpus), attached to the lateral surface of the testis. The head of the epididymis is located at the cranial extremity of the testis; the epididymal tail is at the caudal end of the testis, and differentiates into the ductus deferens which extends into the peritoneal cavity through the processus vaginalis. The ductus deferens loops over the ureter and extends posteriorly to the prostate gland at the base of the bladder.

The mean dimensions of the right testis, with attached epididymis, were length (68 ± 5.6 mm) × height (22 ± 3.5 mm) × width (31 ± 3.1 mm), and mean weight was 24 ± 4.7 g (17 post-pubertal males collected between July/August–January/Febuary). Gonads from harem bulls were not available for analyses.

Age at puberty

The epididymal tubules of seals < 2 years of age were aspermatic. The youngest male in which sperm was observed in both the seminiferous and epididymal tubules was 2 years 10 months old. All males 3 years of age had attained puberty (Fig. 8.2).

Testes weight and volume of post-pubertal males

Growth in body weight with age is presented in Table 8.1. Body weight of 59 post-pubertal males ranged from 59 to 289 kg. Therefore, it was necessary to adjust for body weight when examining seasonal fluctuations in mean testis weight and testis volume (i.e., log body weight was treated as a covariate of log testis weight and log testis volume). It is important to note that because males of the same age may be of different sizes, and individual weights may vary seasonally (see Schusterman & Gentry, 1971), the calculation of seasonal fluctuations in mean testis weight and volume is more complex than is presented in this study.

Mean testis weight differed significantly between the spring/summer (22 September–21 March) and autumn/winter (22 March–21 September) seasons ($F_{1,46} = 9.9$; $P = 0.003$). Testis weights increased in July, remained high throughout the pupping/mating season (November–December), declined in February (post-breeding), and remained low until the following June (Fig. 8.3a). A second, insignificant increase in mean testis weight was observed in March. When younger animals (5–7 years) were excluded from the analysis, observed seasonal trends remained significantly different ($F_{1,23} = 14.7$; $P < 0.001$).

This seasonal trend was also evident in mean testis volume ($F_{1,47} = 2.5$; $P = 0.123$). Although testis volumes were also low from February to June, they increased continually until October, but then declined towards the end of the pupping/mating season (Fig. 8.3b). Change in mean testis volume was primarily attributed to fluctuation in testis length ($F_{1,49} = 10.5$; $P = 0.002$) and width ($F_{1,49} = 8.2$; $P = 0.006$) which increased with the onset of spermatogenesis. Seasonal fluctuation in testis height was minimal.

The annual cycle of the seminiferous and epididymal tubules

Mean diameter of the seminiferous ($F_{1,56} = 12.0$; $P = 0.001$) and epididymal tubules ($F_{1,56} = 28.3$; $P < 0.001$) differed significantly between the spring/summer and autumn/winter seasons. Seminiferous tubule diameters peaked in October (arrival of males at the rookeries), remained high throughout the pupping/mating season (November/December), declined in January/February (post-breeding), and remained low until the following June (Fig. 8.4a). Epididymal tubule diameters were high from September to December, declined in January, and remained low until August (Fig. 8.4b).

The spermatogenic cycle

Inactive

After breeding, from February to the end of June, the testes of all males had regressed, with the exception of one 9-year old male collected in March. Six (24%) of the testes of reproductively regressed males ($n = 24$) were inactive. Seminiferous tubules of inactive testes contained only spermatogonia and Sertoli cells, although a limited number of round primary spermatocytes were present in some tubules (Fig. 8.5a). Strands of Sertoli cell cytoplasm and cellular debris filled the lumen. Tubule diameter was minimal. A considerable amount of connective tissue surrounded individual tubules and the nuclei of Leydig cells were small. Epididymal tubules were devoid of sperm (Fig. 8.6e).

Early spermatogenesis

The first signs of spermatogenic activity were observed in July. Tubules contained several rows of round spermatids (Fig. 8.5b) and sperm was absent from the epididymis. Seminiferous and epididymal tubule diameters, and testis weight and volume, increased during this period (Figs 8.3 & 8.4). Sperm had already accumulated in the epididymes of two 6-year old animals (i.e., late spermatogenesis). By August, sperm were present in the epididymis of 4 of the 5 males examined (Fig. 8.6f). The nuclei of hormone-producing Leydig cells had increased significantly in size from 6.3 ± 0.9 µm (June) to 8.1 ± 1.7 µm (August) ($F_{1,7} = 58.8$; $P < 0.001$).

Late spermatogenesis

From July/August to December/January, all stages of germ cell development were observed (Figs 8.5c–f & 8.6a). Sertoli cells were elongated, extending from the basal lamina to the base of maturing spermatids. From July to the onset of the breeding season testis weight, testis volume and seminiferous tubule diameter increased steadily (Fig. 8.3 & 3.4). The seminiferous tubules were closely packed (little connective tissue) and Leydig cells were enlarged. However, towards the end of the breeding season spermatogenic cells began to show varying degrees of epithelial regression and a slight decrease in testis weights.

Epithelial regression

From February to June, the testes of all males had regressed (Fig. 8.6b–c) with the exception of one 9-year old male collected in March. The diameter of the seminiferous tubules was minimal and there was a corresponding decrease in mean testis weight and volume. Epithelial height was greatly reduced. Spermatids and spermatocytes were eliminated into the lumen and often fused to form multinucleated giant cells comprising 8–31 nuclei (Fig. 8.6d). Giant cells were observed from December to June, but were not evident in all sections. Sperm was absent from the epididymis during this period. The transition phase between epithelial regression and inactivity was not established, yet started as early as February in one 10-year old male.

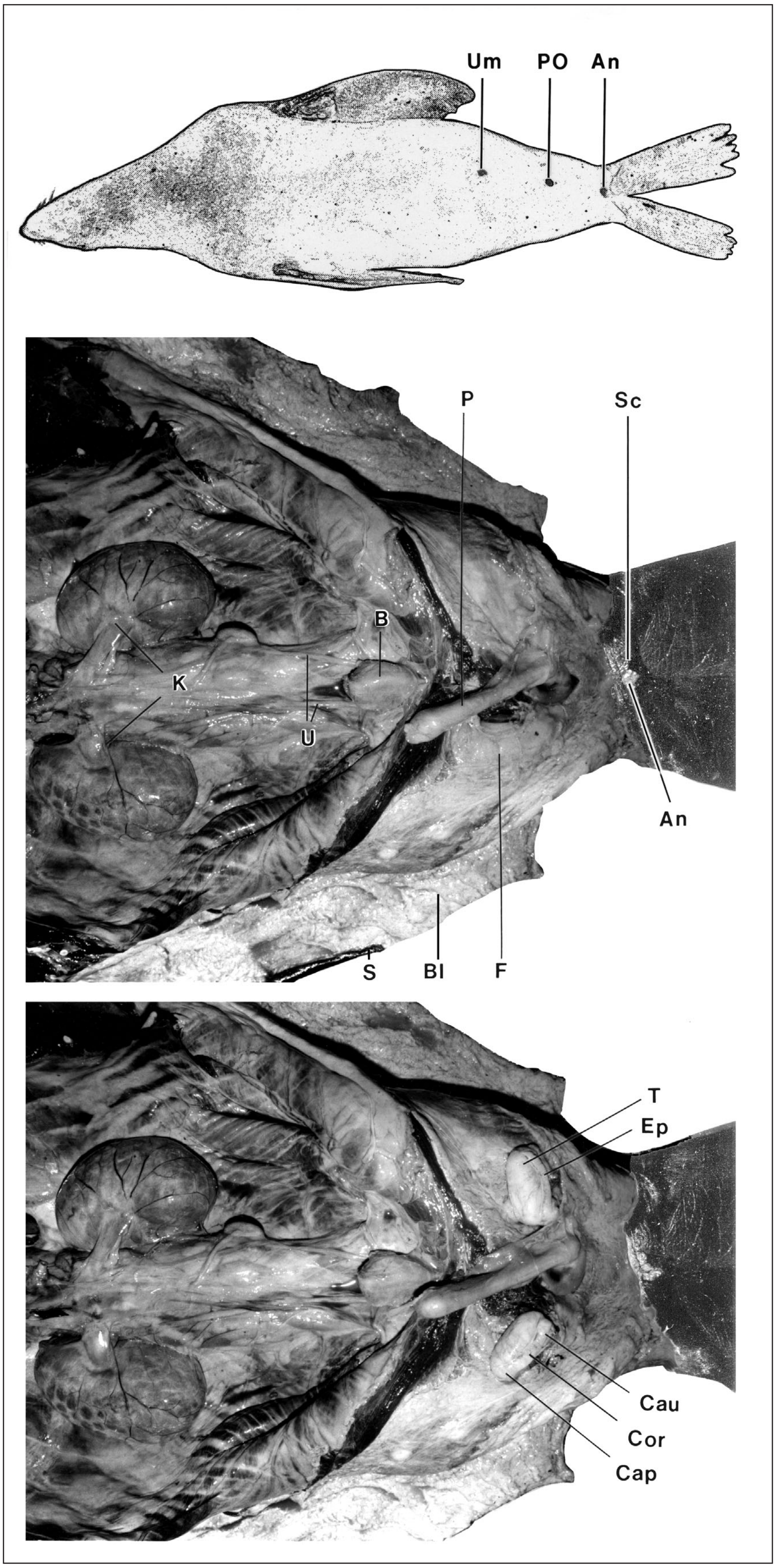

Fig. 8.1 Reproductive tract of an 8-year old male *A. p. pusillus* collected in July showing appearance of genital opening and orientation of the testes.

Anus (An); bladder (B); blubber (Bl); epididymis (Ep): Cap, Caput; Cor, Corpus; Cau, Cauda; fascia (F); kidney (K); penis (P); penial opening (PO); skin (S); scrotum (Sc); testis (T); ureter (U); umbilicus (Um).

Table 8.1 ***Growth in body weight and testis weight with age in male A. p. pusillus (n = 99 seals)***

Mean age[a] (years)	**No. of males**	**Body weight[b] (kg) ± S.D.**	**Right testis weight[c] (g) ± S.D.**
1	3	12 ± 5	1.2 ± 0.2
2	5	20 (2)	2.2 (2)
3	19	52 ± 13 (7)	14.1 ± 0.3 (7)
4	15	59 ± 10 (12)	18.9 ± 0.5 (13)
5	4	75 (2)	24.5 ± 11.3 (3)
6	12	84 ± 12 (11)	18.4 ± 12.5 (11)
7	6	100 ± 24	19.9 ± 5.1 (5)
8	9	116 ± 35	21.0 ± 4.0
9	7	119 ± 18 (6)	20.0 ± 4.6
10	4	125 ± 30	19.6 ± 1.3 (3)
11	4	139 ± 48	24.0 ± 8.3
12	4	154 ± 41	25.0 ± 5.8 (3)
13+	3	212 (2)	26.4 (1)
Total[d]	**95**		

[a] Age was estimated from tooth sections; all males < 4 years of age (*n* = 21) had been tagged within 6 weeks of birth and were therefore of known-age.

[b] Body weights and testes weights were not available for all males. Sample sizes are indicated in parentheses.

[c] Testis weights = each right testis with attached epididymis.

[d] No upper canines for 4 post-pubertal males (i.e., total = 99 males of which 95 were aged).

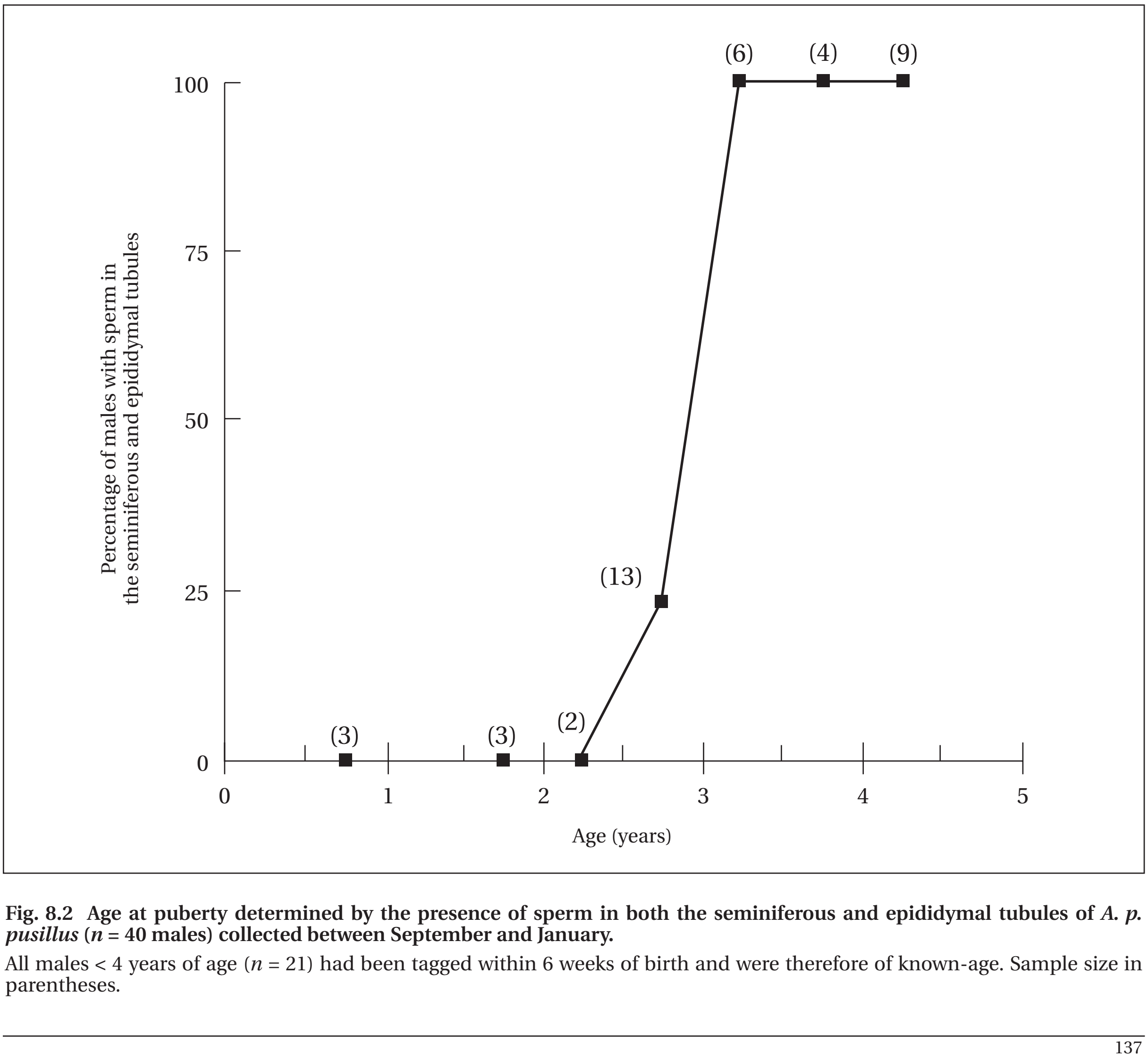

Fig. 8.2 Age at puberty determined by the presence of sperm in both the seminiferous and epididymal tubules of *A. p. pusillus* (*n* = 40 males) collected between September and January.

All males < 4 years of age (*n* = 21) had been tagged within 6 weeks of birth and were therefore of known-age. Sample size in parentheses.

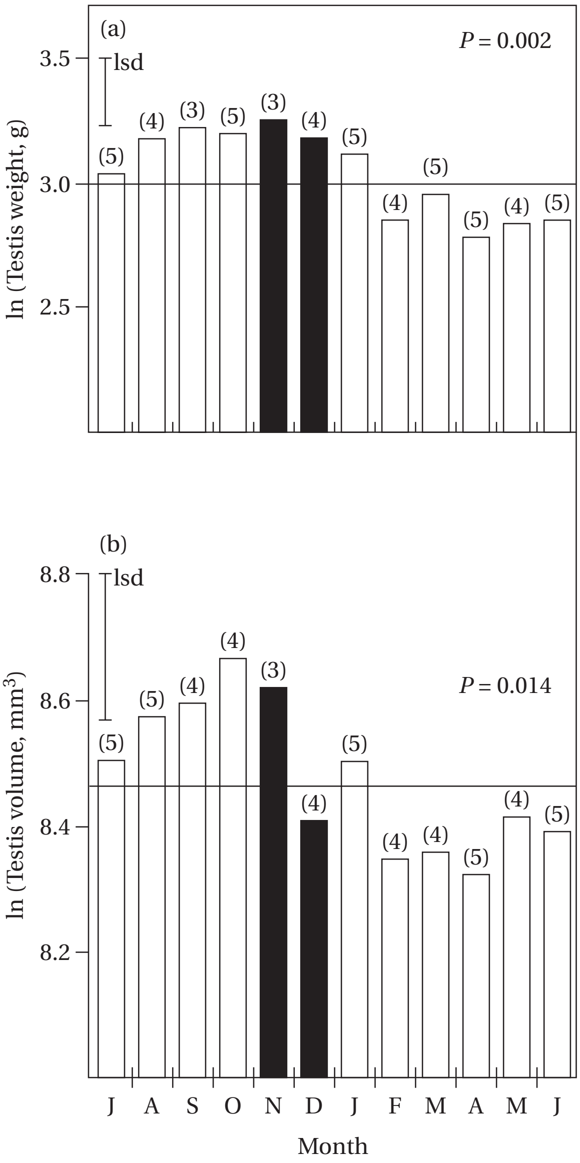

Fig. 8.3 Mean monthly (a) testis weight and (b) testis volume in post-pubertal *A. p. pusillus*.

Mean values were obtained from the right testis with attached epididymis. Body weight of seals ranged from 59 to 289 kg, therefore it was necessary to adjust for body weight (i.e., log body weight was treated as a covariate of log testis weight and log testis volume). Sample sizes in parentheses; solid bars, pupping/mating season; horizontal line, grand means.

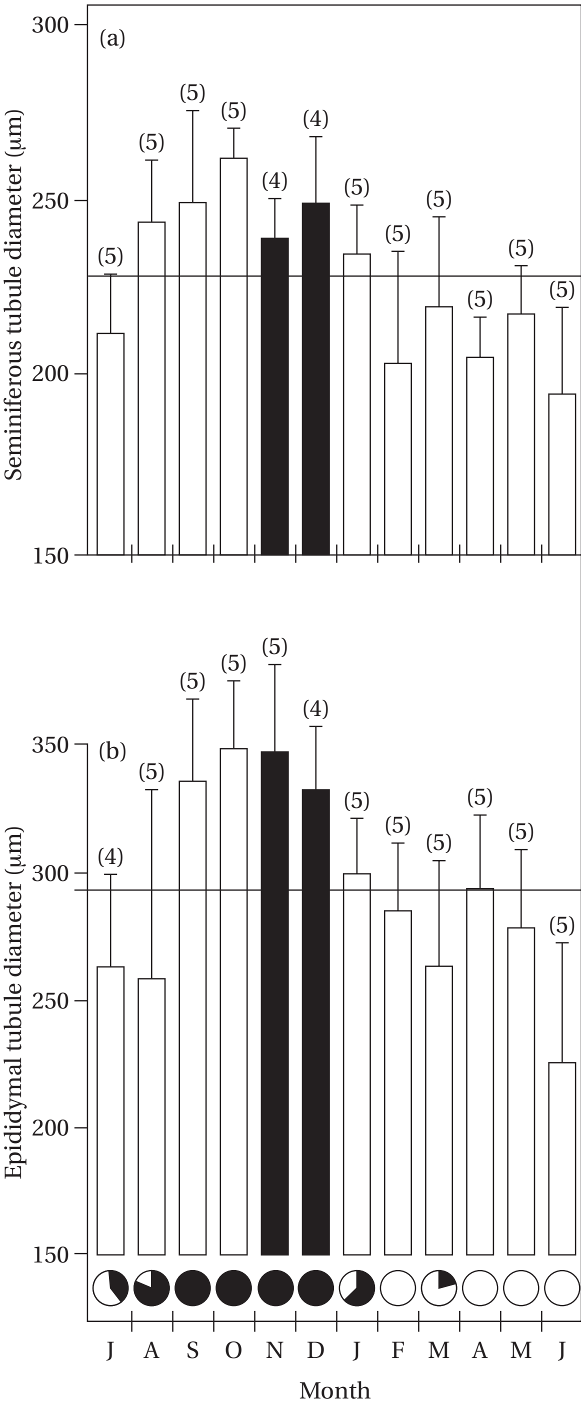

Fig. 8.4 Mean monthly diameter of (a) seminiferous tubules and (b) epididymal tubules in post-pubertal *A. p. pusillus*.

Vertical bars are 1 sample standard deviation. Sample sizes in parentheses; solid bars, pupping/mating season; horizontal line, grand means. The presence of sperm in the epididymis is indicated in fifths: (●) Spermatozoa present in the seminiferous and epididymal tubules of all males; (○) No spermatozoa.

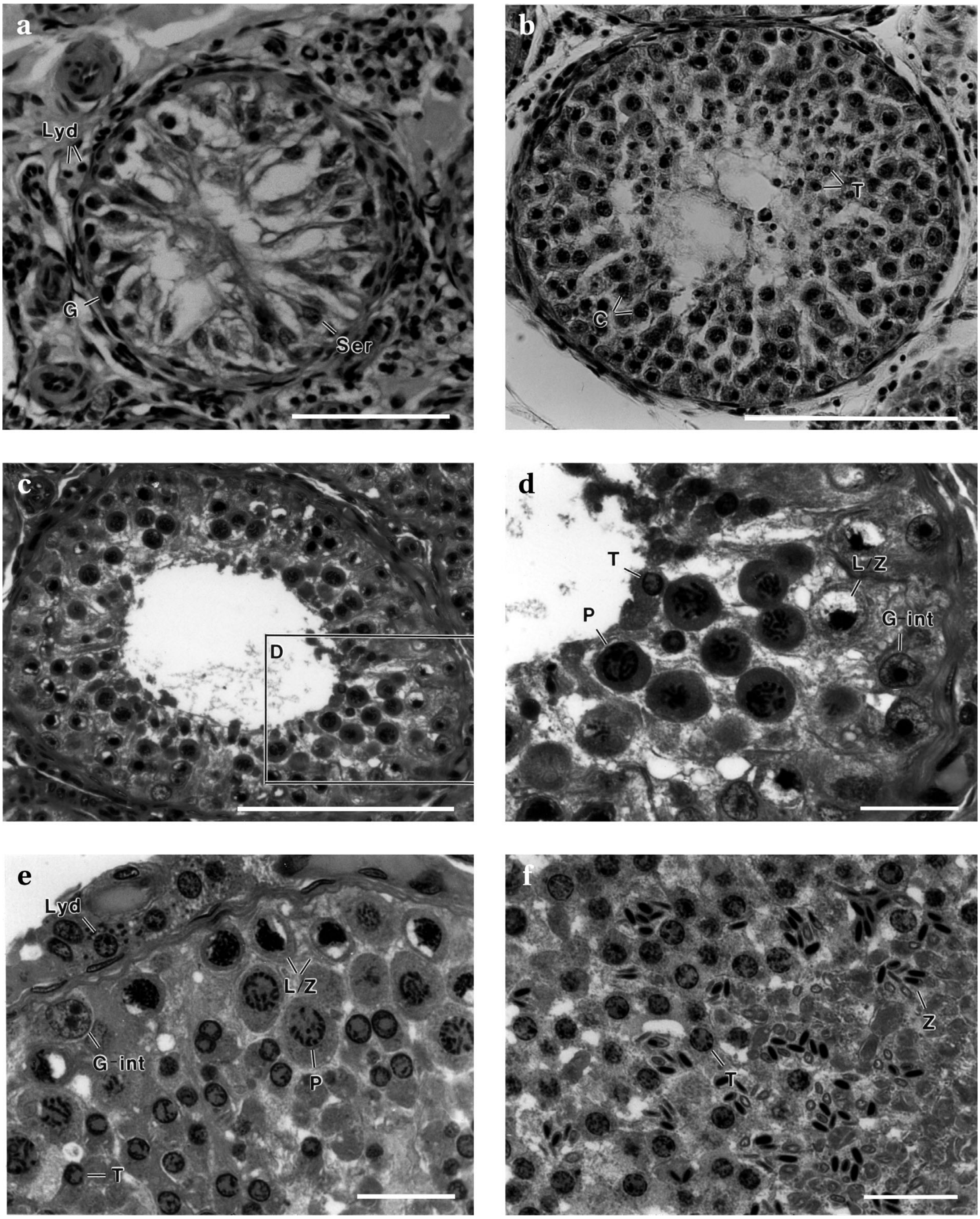

Fig. 8.5 Histological sections of the testis in post-pubertal *A. p. pusillus* collected during the breeding and non-breeding season.

(a) Inactive: seminiferous tubule collected in April showing Sertoli cells (Ser), type Ad spermatogonia (G) and strands of Sertoli cell cytoplasm within the lumen; Leydig cells (Lyd) small.

(b) Early spermatogenesis: seminiferous tubule (July) showing primary spermatocytes (C) with condensed nuclear chromatin and several rows of young spermatids (T).

(c–f) Active spermatogenesis: (c–d) seminiferous tubule showing spermatogonia in interphase (G-int); leptotene/zygotene (L/Z) and pachytene (P) division of primary spermatocytes, and young spermatids (T); (e) differentiation of primary spermatocytes; spermatogonia in interphase (G-int); leptotene/zygotene (L/Z) and pachytene (P) stages of primary spermatocytes and a large number of young spermatids (T); Leydig cells (Lyd) enlarged; (f) spermiogenesis showing spherical nuclei of young spermatids (T) and elongated nuclei of maturing spermatids (Z).

Scale bars: a–c = 50 μm; d–f = 10 μm. H & E = a–b; Toluidine = c–f.

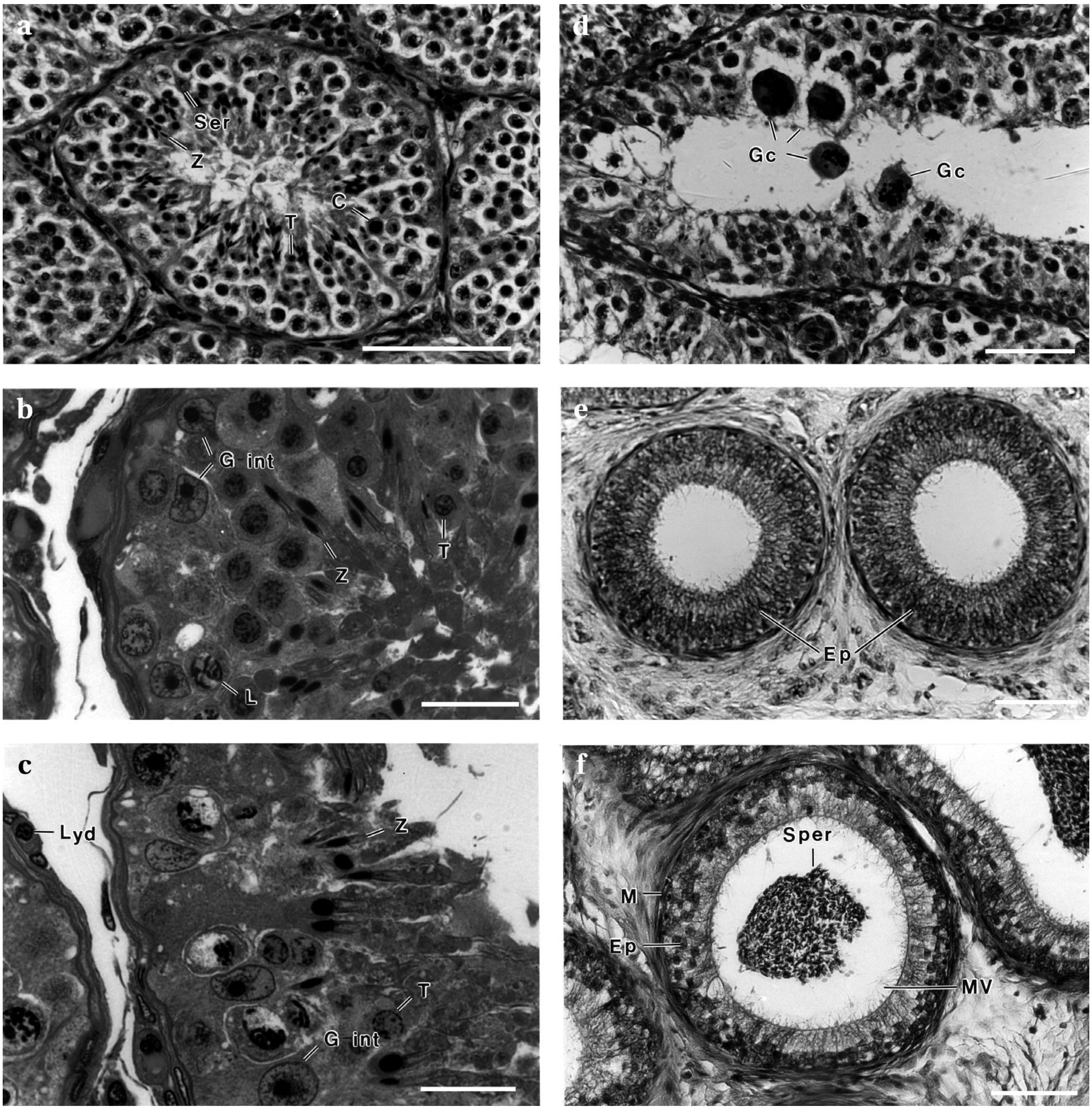

Fig. 8.6 Histological sections of the testis and epididymis in post-pubertal *A. p. pusillus* collected during the breeding and non-breeding season.

(a) Late spermatogenesis: seminiferous tubule (November) showing maturing spermatids (Z); individual Sertoli cells (Ser) extend from the basement membrane to the heads of elongating spermatids and are surrounded by irregular columns of spermatocytes (C) and round spermatids (T); scale bar = 50 µm.

(b–d) Epithelial regression: (b–c) seminiferous tubule (February) showing spermatogonia in interphase (G-int); leptotene (L) stages of primary spermatocytes and mature spermatids (Z); spermatogenic cells have decreased in number and the lumen is filled with Sertoli cytoplasm; Leydig cells (Lyd) are small and irregular in shape; scale bar = 20 µm; (d) regressed seminiferous tubule (February) showing depletion of the germinal epithelium and the formation of giant cells (Gc); scale bar = 80 µm.

(e–f) Epididymis: (e) Epididymis (June); tubule diameter small, lumen area reduced and columnar epithelium height at a maximum. Note the absence of sperm; scale bar = 50 µm; (f) Epididymis (November); tubule diameter large, lumen wide and columnar epithelium height reduced; note the accumulation of sperm (Sper) within the lumen, tall microvilli (MV) and narrow band of circular muscle fibre (M); scale bar = 50 µm.

H & E = a & d–f; Toluidine = b–c.

DISCUSSION

The gross anatomy of the male reproductive tract conforms with the standard otariid pattern described by Laws & Sinha (1993); however, the position of the testes is variable. The position of the testes is a characteristic feature used to distinguish otariids (i.e., testes scrotal) and phocids (i.e., testes inguinal). The testes of the Cape fur seal are generally withdrawn into the groin and covered by a layer of blubber and fascia, protected within the cremasteric pouch, the anterior section of the scrotum. The scrotum appears to be fully pendulous only when the testes descend from the pouch, when the seal is in prime 'breeding condition', actively defending territory; or when the seal is suffering heat stress (see Laws & Sinha, 1993). Within the scrotum, the testes are at least 6˚C below body temperature (Bartholomew & Wilke, 1956). Thus, externalization of the testes may optimize sperm production during long periods of territorial tenure, when fighting and sunny conditions elevate body temperature.

It has now been established that male *A. p. pusillus* reach puberty between 3 and 4 years of age. By comparison, male *A. gazella* attain puberty at 3–4 years of age (McCann & Doidge, 1987), *A. tropicalis* at ≥ 4 years (Bester, 1990) and *Arctocephalus pusillus doriferus* at 4–5 years (Warneke & Shaughnessy, 1985). In captive populations, male Cape fur seals are capable of fertilising receptive females at 4 years of age (Linda Clokie-Van Zyl, pers. comm.), which supports the estimated age at puberty arrived at in the present study.

In wild populations, male Cape fur seals do not have the ability to acquire and maintain a harem until they are approximately 10–14 years of age (David, 1989). Large body size and the ability to gain high social rank may contribute to the lifetime reproductive success of this polygynous breeding species (see Bartholomew, 1952, 1970; Le Boeuf & Peterson, 1969; Le Boeuf *et al.,* 1972; Le Boeuf, 1974, 1981; Miller, 1975; Cox & Le Boeuf, 1977; Le Boeuf & Briggs, 1977; McCann, 1980; Anderson & Fedak, 1985; Le Boeuf & Reiter, 1988; Deutsch *et al.,* 1990; Andersson, 1994). The estimated maximum longevity of the male Cape fur seal is at least 20 years of age (Wickens, 1993). During this time, a male may mate multiple times over a 2 to 3 year period (Gentry & Kooyman, 1986), or longer (Oosthuizen, pers. obs). Although little is known of changes in fertility with age, it is likely that males die before reaching reproductive senescence (e.g., Laws, 1956). Although few males ≥ 12 years of age ($n = 7$) were collected in this study, histological examination of the testes did not suggest a decline in sexual activity with age.

The seasonal cycle of the testis in adult *A. p. pusillus* is similar to many other temperate, seasonal breeding mammals (Sadleir, 1969). A significant increase in both testicular mass and tubule dimensions reflects a fertile period extending from July/August to December/January. Comparison of quiescent and active testes suggested that Leydig cell activity increased with the onset of spermatogenesis. Although some males may remain active until March (e.g., one 9-year old male), the absence of spermatozoa in the epididymis during February to June, when mean testis mass and mean tubule diameter reached a minimum, clearly showed that *A. p. pusillus* males were quiescent shortly after the rut. Similar findings were reported in *A. tropicalis*; fertile periods extended from September/October to January/Febuary, with some individuals also remaining active until March (Bester, 1990). Although species at higher latitudes generally have shorter breeding seasons (Gentry *et al.*, 1986), *A. tropicalis* (38–48˚ lat.) in fact has a slightly longer breeding season (i.e., November to early January) than *A. p. pusillus* (18–34˚ lat.); therefore, it is not unexpected that the duration of male fertility is similar in the two species.

Four stages of spermatogenesis were observed: (1) inactive (February/March–June); (2) early spermatogenesis (July); (3) late spermatogenesis (July/August–December/January) and (4) epithelial regression (February–June). Germ cell proliferation appeared to follow the normal mammalian pattern (Guraya, 1987), but the transition stage between epithelial regression and inactivity was not as well defined as for Antarctic phocids (Laws, 1956). These two stages, although distinctly different, overlapped in time (i.e., February to June). Only six of the 24 reproductively regressed males collected between February and June were inactive; one 9-year old was active ($n = 25$). Individual variation between males, particularly differences in social status and body condition, may influence the interval between reproductive regression and inactivity (e.g., Laws, 1956; Vivier & Van der Merwe, 1996). Harem bulls may fast for up to 40 days, and then abandon their territories when they have exhausted their physiological reserves; if they cannot replenish them quickly, they will die (Wartzok, 1991). In contrast, younger males or subordinates do not fast so rigorously; therefore, may remain in breeding condition longer than harem bulls.

Large breeding bulls (up to 350 kg) arrive at the rookeries late October/early November (Rand, 1967) and are therefore in breeding condition (this study). Pregnant females gather in high densities shortly afterwards to find suitable pupping sites. Mean harem size is variable and ranges from approximately 3–28 females (Rand, 1972). Females give birth to a single black pup within 1–2 days of coming ashore. Ninety percent of pups are born over a 34-day period and mating occurs 6 days post-partum (Shaughnessy, 1979). David & Rand (1986) reported 90% of births in a 26-day period in Namibia. Spatial separation of food resources from the breeding rookeries requires males to fast in order to ensure access to receptive females (Boness, 1991). Bulls may stay ashore without feeding for up to 40 days (Rand, 1967). Large body size enables breeding bulls to remain on territory for extended periods (i.e., metabolize extensive blubber stores), and also provides a direct advantage in competitive interactions (i.e., greater strength) (Rand, 1967; Bartholomew, 1970; Wartzok, 1991). The territorial system gradually breaks down in late December/early January as dominant bulls return to sea to replenish their physiological reserves (Rand, 1967). This period marks the onset of epithelial regression and finally a decline in testes volume and weight (this study).

Although no harem bulls were collected in this study, socially mature males (≥ 12 years of age) have larger gonads, in relation to body weight, than younger males (Table 8.1). Large gonad size would facilitate the production and storage of large quantities of sperm, enabling harem bulls to service many females within a short time (i.e., within 26–34 days) (Rand, 1967; David & Rand, 1986). The adaptations allowing for production of large quantities of sperm over a short period have not been investigated in pinnipeds (Wartzok, 1991); however, Bartholomew & Hoel (1953) found that harem bulls are able to produce sufficient sperm to maintain high levels of conception in females (e.g., 161 northern fur seal females were mated by a single male). It is possible that Cape fur seals achieve a similar high level of polygyny in some colonies (David, 1987*b*; Boness, 1991).

It is generally believed that photoperiod is a proximate control factor in the annual cycle of pinniped reproduction (Boyd, 1991; 1996). Synchronized breeding is mediated through the pineal-pituitary axis and gonadotrophic action which varies according to species and latitude (Daniel, 1981; Griffiths & Bryden, 1981). When calculating mean monthly day length between 32˚ S and 34˚ S (the latitudinal band in which the majority of *A. p. pusillus* were collected) it is apparent that early spermatogenesis coincides with the initial increase in day length (July = 10 h 9 min) following the winter solstice (21–22 June), and pupping/mating coincides with the longest days (November = 13 h 52 min; December = 14 h 21 min). A second (non-significant) peak in testis weight was recorded in March (autumnal equinox), when the majority of males come ashore to moult. In *A. p. pusillus*, the adult moult extends from late January to mid-April, and peaks in early March (Warneke & Shaughnessy, 1985). Photoperiodic cueing is also thought to explain seasonal reproductive trends in male *M. leonina* (Griffiths, 1984*a*) and *A. tropicalis* (Bester, 1990).

Cape fur seals inhabit a temperate, moderately seasonal clime, dominated by areas of coastal upwelling and cold oceanic currents (Shannon, 1985). Their breeding cycle is shaped by reduced seasonality and unpredictable, yearly fluctuations in marine productivity (e.g., El Niño events/Southern Oscillations) (Cane, 1983). Inshore on the west and south coasts, primary productivity is maximal in spring (September-November) and summer (December-February), when wind-induced upwelling is intense (Azam *et al.*, 1983; Shannon, 1985; Brown, 1992). It is during this period that Cape fur seals give birth (summer) and generally wean their pups (spring). Females suckle their young for 9–11 months, during which time they make many foraging trips to sea of short duration (David & Rand, 1986). If food resources are abundant, close to the rookery, lactating females would spend less time away from their pups, increasing the probability of reproductive success (Majluf, 1992). Thus, the need for abundant food resources after the perinatal fast and during ‘early’ foraging trips to sea may determine the timing of birth (Majluf, 1992). This is in agreement with Boyd (1996) who suggested that photoperiod is responsible for inducing implantation in Antarctic fur seals, and that the duration of pregnancy is increased in years associated with low availability of food (i.e., later births). Considering that 90% of Cape fur seal pups are born over a 34-day period from November to late December, and mating occurs 6 days post-partum (Shaughnessy, 1979), reproduction in the male is thus geared to coincide with the short summer oestrus. Spermatogenesis begins 3–4 months before the breeding season (this study) to enable complete maturation of the testis (Setchell, 1978) and to cover any small temporal shifts in the receptiveness of females during the brief breeding season.

In conclusion, we have established that male Cape fur seals reach puberty at between 3 and 4 years of age and that bulls are seasonally active, with spermatogenesis ending shortly after the rut, and it is suggested that the regular cue of photoperiod entrains reproduction. Further studies addressing: (i) the relationship between growth in body weight and sperm accumulation in the epididymis; (ii) seasonal changes in reproductive endocrinology; and (iii) age at reproductive senescence, would greatly improve our understanding of reproduction in this species. Long-term studies documenting the seasonal distribution and abundance of prey species in relation to the energetics of lactation are required to test the hypothesis that reproductive synchrony may be largely determined by food availability in the summer months.

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PART 5

GENERAL BIOLOGY
DIET AND FORAGING

CHAPTER 9

Diet and foraging behaviour of the Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae) from the Eastern Cape coast of South Africa

INTRODUCTION

The Cape (South African) fur seal, *Arctocephalus pusillus pusillus*, occurs only on the coasts of South Africa and Namibia, and is the only resident seal species in southern Africa. Breeding rookeries are distributed from Black Rocks (33º50'S, 26º16'E) in Algoa Bay, on the south east coast of Southern African, to Cape Cross (21º46'S, 13º58'E) in Namibia. The majority of seals occur on the west coast. The remainder of the population (*c.* 8.5%; 140 000 seals in 1993; J.H.M. David, pers. comm.) inhabits the south/east coast, between False Bay and Algoa Bay, at five breeding colonies and one non-breading colony. Their distribution overlaps important commercial fishing grounds.

Cape fur seals feed predominantly on teleost fish, and to a lesser extend cephalopods, with crustaceans forming a relatively minor part of the diet (Rand, 1959; David, 1987; Lipinski and David, 1990; Castley *et al.*, 1991). On the south coast of southern Africa, teleost fish contribute 67.7% to the diet, cephalopods 29.7%, crustaceans 1.2% and elasmobranchs 1.2%; and the most important prey species are anchovy (*Engraulis capensis*), horse mackerel (*Trachurus trachurus capensis*), pilchard (*Sardinops ocellatus*) and hake (*Merluccius capensis; M. paradoxus*)(*n* = 115 stomachs) (David, 1987).

Some of the more common species eaten by Cape fur seals are of commercial importance. Subsequently, many fishermen have adopted a negative attitude towards seals. Recently, fishing effort in Eastern Cape waters (Plettenberg Bay, 33º 07'S, 23º25'E, to the Kwazulu-Natal boarder, 31°05'S, 30°11'E) has increased significantly, particularly that for line fish, and chokker squid (*Loligo vulgaris reynaudii*). In 1992–1995, 234–254 squid vessels and 403–438 line fish vessels operated between Port Alfred and Mossel Bay[1]. White squid grossed between R46,236,024.00–R118,909,710.00 per annum, and line fish grossed between R9,459,522.00–R16,600,173.00 per annum[1]. In addition, *c.* 10 inshore trawlers and *c.* 6 deep sea trawlers operated in the area, targeting mainly hake and horse mackerel.

The effects of increased fishing efforts on the local seal population are unknown, but unlike the west coast population, that on the Eastern Cape coast is not increasing. Considering that the reduction in prey populations have been implemented in the decline of several species of otariids, including the northern fur seal (*Callorhinus ursinus*) (Loughlin, 1991), and the Steller's sea lion (*Eumetopias Jubatus*) (Loughlin, 1991; Trites & Larkin, 1992), it is necessary to obtain quantitative information on the diet of Cape fur seals in this region. Currently, dietary information is limited to a study of 36 stomachs from stranded (beached) seals collected between 1976 and 1990, in which hake and chokker squid were reported to be the most important prey species (Castley *et al.*, 1991).

In the present study, we document the diet and foraging behaviour of Cape fur seals from the Eastern Cape coast. Specific objectives were to: (i) determine the composition of the diet from: faecal samples/regurgitates collected from breeding and non-breeding colonies; stomachs collected from stranded animals; and stomachs collected from animals incidentally entrapped in commercial trawl nets; (ii) investigate the potential for competition between seals and the commercial fisheries; and (iii) document diving behaviour and movement patterns, using satellite telemetry.

MATERIALS AND METHODS

Collection of food samples from faeces and regurgitates

Fresh faecal samples, which showed no obvious signs of desiccation, were collected in polythene bags from non-breeding (Rondeklippe, Plettenberg Bay) and breeding (Black Rocks, Algoa Bay) colonies. Faecal samples were not always found in discrete units therefore, all samples obtained during a designated collection trip were pooled and treated as a single sample.

At Rondeklippe, fresh faecal samples were usually collected several times a month between June 8, 1993 and November 6, 1995 (Table 9.1). Three to six samples were collected per field trip (*n* = 64 field trips).

At Black Rocks, faecal samples were collected on an opportunistic basis between May 11, 1992 and November 11, 1995 (Table 9.2). Five to twenty samples were collected per field trip (*n* = 13 trips). At Black Rocks, samples included regurgitated material and material dredged from rock pools.

Table 9.1 ***Monthly distribution of faecal samples (n = 64) collected at Rondeklippe colony, Plettenberg Bay, between June 1993 and November 1995***

Season	**Month**	**Year**		
		1993	**1994**	**1995**
Summer	Dec.	1	0	–
	Jan.	–	1	0
	Feb.	–	0	4
Autumn	Mar.	–	3	3
	Apr.	–	3	3
	May	–	2	0
Winter	Jun.	3	0	3
	Jul.	5	0	6
	Aug.	3	1	1
Spring	Sep.	3	2	2
	Oct.	2	5	1
	Nov.	3	3	1
		20	**20**	**24**

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[1] This data was extracted from the National Marine Linefish System (NMLS) based on data provided by the permit holders on a monthly basis (Chris Wilke, pers. comm.).

Table 9.2 ***Monthly distribution of faecal samples and regurgitations (n = 13) collected at Black Rocks seal colony, Algoa Bay, between May 1992 and November 1995***

Season	**Month**	**Year**			
		1992	**1993**	**1994**	**1995**
Summer	Dec.	–	1	1	–
	Jan.	–	–	–	1
	Feb.	–	–	1	–
Autumn	Mar.	–	2	–	–
	Apr.	–	–	–	–
	May	1	–	–	1
Winter	Jun.	–	–	–	–
	Jul.	–	–	–	–
	Aug.	–	–	–	1
Spring	Sep.	–	–	1	–
	Oct.	–	–	1	–
	Nov.	–	1	–	1
		1	**4**	**4**	**4**

One sample = all faeces/regurgitates collected during one sampling trip.

Collection of food samples from stomachs

A total of 41 stomachs were collected from Cape fur seals stranded (beach dead) off the Eastern Cape coast between January 1991 and December 1995. An additional 37 stomachs were collected from seals incidentally entrapped in trawl nets during commercial fishing operations off the Eastern Cape coast between July 1992 and August 1995. Details of animals which had prey remains in their stomach are presented in Table 9.3 and 9.4.

Standard necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). Stomachs were excised, ligatured at the oesophageal and duodenal ends, and placed on ice (1–4 days), or chilled in a cold room (4°C) overnight before examination.

In the laboratory, stomachs were weighed and then incised longitudinally. Food items were flushed from the stomach through nested sieves (2 mm; 0.5 mm) over a large tray. Fish otoliths were removed from skulls. Whole fish and fish pieces were identified where possible, measured and weighted. Otoliths, cephalopod beaks, crustacea and other food items were sorted and preserved for further analysis. Otoliths were stored in gelatin capsules; other material was stored in 70% ethanol. Empty stomachs were then weighed to calculate content mass.

All faecal samples/regurgitates were soaked in a solution of one part liquid detergent to 100 part water overnight, and were then washed through nested sieves (2 mm; 0.5 mm). Food material remaining in the sieve was sorted and preserved (as above) for further analysis.

Identification and analysis of food samples

Otoliths and cephalopod beaks were identified to the lowest taxon possible with the aid of published keys (Clarke, 1986; Smale *et al.,* 1993; Smale *et al.,* 1995), and reference specimens held at the Port Elizabeth

Table 9.3 ***Stranded (beached) Cape fur seals collected off the Eastern Cape coast between January 1991 and December 1995 with prey remains in their stomach***

	ID No.	**Date of collection**	**Approximate location**	**Sex**	**Length[a] (cm)**
1.	PEM1829	13 Jan 91	Seaview (34° 01’S, 25° 17’E)	M	–
2.	PEM1832	14 Mar 91	Cape Recife, PE (34° 02’S, 25° 42’E)	M	205
3.	PEM1840	26 May 91	*c.* 1 km W of Cape Recife	–	–
4.	PEM1841	26 May 91	*c.* 1 km W of Cape Recife	M	222
5.	PEM1868	24 Sep 91	Cape Recife, PE (34° 02’S, 25° 42’E)	M	199
6.	PEM1890	13 Jul 92	Cape Recife, PE (34° 02’S, 25° 42’E)	M	192
7.	PEM2057	28 Jun 93	Pollock Beach, PE (33° 59’20”S, 25° 40’ 30”E)	M	172
8.	PEM2087	17 Aug 93	Plettenberg Bay (34° 07’S, 23° 25’E), Robberg	M	190
9.	PEM2137	5 Jan 94	Summerstrand, PE (34° 00’S, 25° 42’E)	M	118
10.	PEM2141	17 Jan 94	39 km E of Sundays River Mouth, WC	M	198
11.	PEM2143	21 Jan 94	Seaview (34° 01’S, 25° 17’E)	M	189
12.	PEM2186	7 Apr 94	Amsterdamhoek (33° 52’S, 25° 38’E)	M	90
13.	PEM2191	4 May 94	Port Alfred (33° 36’S, 26° 55’E)	M	100
14.	PEM2198	Jul 94	Plettenberg Bay (34° 03’S, 23° 24’E)	M	105
15.	PEM2203	18 Jul 94	Port Elizabeth Harbour (33° 58’S, 25° 37’E)	M	204
16.	PEM2204	23 Jul 94	Maitland River Mouth (33° 59’S, 25° 18’E)	F	86
17.	PEM2261	Nov 94	Cape Recife, PE (34° 02’S, 25° 42’E)	M	118
18.	PEM2348	14 Nov 94	Humewood, PE (33° 59’S, 25° 40’E)	M	189
19.	PEM2379	12 Apr 95	Bokness (33° 41’S, 26° 31’E)	M	189
20.	PEM2454	8 Nov 95	Noordhoek (34° 02’S, 25° 39’E)	M	196
21.	PEM2458	3 Dec 95	Cape St. Francis (34° 12’S, 24° 52’E)	M	110

An additional 20 stomachs were examined which were empty (PEM1882, PEM1885, PEM1900, PEM1901, PEM2018, PEM2049, PEM2081, PEM2134, PEM2140, PEM2155, PEM2201, PEM2238, PEM2248, PEM2350, PEM2359, PEM2374, PEM2402, PEM2403, PEM2404 and PEM2405).

[a] Standard body length (tip of snout to tip of tail with animal lying on its back).

Table 9.4 *Cape fur seals incidentally entrapped in trawl nets during commercial fishing operations off the Eastern Cape coast between July 1992 and August 1995 with prey remains in their stomach*

	ID No.	Date of collection	Approximate location	Sex	Length (cm)
1.	PEM1999	20 Jul 92	EC trawl grounds (34° 52’S, 23° 35’E–34° 50’S, 23° 48’E)	M	155[b]
2.	PEM2000	21 Jul 92	EC trawl grounds (34° 50’S, 23° 48’E–34° 48’S, 24° 00’E)	M	146[b]
3.	PEM2002	22 Jul 92	EC trawl grounds (34° 55’S, 23° 14’E–34° 53’S, 23° 26’E)	M	163[b]
4.	PEM2003	24 Jul 92	EC trawl grounds (34° 51’S, 23° 42’E–34° 49’S, 23° 53’E)	M	145[b]
5.	PEM2004	25 Jul 92	EC trawl grounds (34° 45’S, 24° 18’E–34° 48’S, 24° 00’E)	M	194[b]
6.	PEM2005	11 Aug 92	EC trawl grounds (34° 43’S, 24° 34’E–34° 40’S, 24° 45’E)	M	145[b]
7.	PEM2006	13 Aug 92	EC trawl grounds 34° 45’S, 24° 25’E–34° 42’S, 24° 40’E)	M	153[b]
8.	PEM2008	14 Aug 92	EC trawl grounds (34° 41’S, 24° 42’E–34° 38’S, 24° 54’E)	M	147[b]
9.	PEM2009	22 Aug 92	EC trawl grounds (34° 41’S, 24° 45’E–34° 37’S, 24° 59’E)	M	148[b]
10.	PEM2010	22 Aug 92	EC trawl grounds (34° 47’S, 24° 11’E–34° 46’S, 24° 25’E)	M	147[b]
11.	PEM2011	8 Sep 92	EC trawl grounds (33° 50’S, 27° 06’E–34° 37’S, 24° 59’E)	M	160[b]
12.	PEM2012	9 Sep 92	EC trawl grounds (34° 40’S, 24° 41’E–34° 39’S, 24° 53’E)	F	162[b]
13.	PEM2013	13 Sep 92	EC trawl grounds (34° 24’S, 25° 50’E–34° 25’S, 26° 02’E)	M	166[b]
14.	PEM2014	25 Sep 92	EC trawl grounds (34° 23’S, 26° 04’E–34° 23’S, 25° 58’E)	M	162[b]
15.	PEM2015	3 Nov 92	EC trawl grounds (34° 17’S, 24° 36’E–34° 20’S, 24° 23’E)	M	158[b]
16.	PEM2046	19 May 93	EC trawl grounds (35° 00’S, 21° 41’E–35° 08’S, 21° 27’E)	M	141[a]
17.	PEM2047	20 May 93	EC trawl grounds (34° 53’S, 23° 27’E–34° 50’S, 23° 40’E)	M	167[a]
18.	PEM2048	20 May 93	EC trawl grounds (34° 53’S, 23° 27’E–34° 50’S, 23° 40’E)	M	157[a]
19.	PEM2051	28 Jun 93	EC trawl grounds (34° 44’S, 24° 29’E–34° 45’S, 24° 20’E)	M	168[a]
20.	PEM2052	28 Jun 93	EC trawl grounds (34° 44’S, 24° 29’E–34° 45’S, 24° 20’E)	M	171[a]
21.	PEM2053	28 Jun 93	EC trawl grounds (34° 46’S, 24° 21’E–34° 44’S, 24° 32’E)	M	153[a]
22.	PEM2054	29 Jun 93	EC trawl grounds (34° 45’S, 24° 28’E–34° 47’S, 24° 18’E)	M	165[a]
23.	PEM2055	29 Jun 93	EC trawl grounds (34° 46’S, 24° 22’E–34° 44’S, 24° 32’E)	M	179[a]
24.	PEM2056	29 Jun 93	EC trawl grounds (34° 46’S, 24° 22’E–34° 44’S, 24° 32’E)	M	139[a]
25.	PEM2082	Jul 93	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	176[a]
26.	PEM2252	22 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	172[a]
27.	PEM2253	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	152[a]
28.	PEM2254	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	146[a]
29.	PEM2256	17 Sep 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	198[a]
30.	PEM2257A	19 Sep 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	142[a]
31.	PEM2257B	7 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	170[a]
32.	PEM2258	8 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	186[a]
33.	PEM2400	13 Jul 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	176[a]
34.	PEM2401	13 Jul	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	146[a]
35.	PEM2414	25 Aug 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	M	148[a]

An additional 2 stomachs were examined which were empty (PEM2001, PEM2007).

[a] Standard body length (from the tip of the snout to the tip of tail with the animal lying on its back).

[b] Curve linear body length (from the tip of the snout to tip of the tail with the animal lying on its back, over the curve of the body).

Museum. Dr. M. Smale and Dr. N. Klages confirmed the identity of specimens which were difficult to key.

Complete otoliths showing no or little sign of erosion were measured under a dissection microscope fitted with an eyepiece micrometer (± 0.01 mm), i.e., maximum length or maximum breadth as appropriate. Cephalopod beaks were measured using vernier callipers (± 0.05 mm), i.e., lower rostral length (LRL) for all squid; and lower crest length (LCL) for all octopus. The dimensions of each otolith and cephalopod beak were used to estimate the original length (total length or dorsal mantle length) and wet mass of the fish and cephalopod prey, using the appropriate regression equations, i.e., Smale *et al.*, 1993; Smale *et al.*, 1995; N. Klages, pers. comm.

In order to determine the number of prey items and the frequency of occurrence of each prey item, two methods were followed. Firstly, all left and right otoliths, and all upper and lower cepahlopd beaks, were counted. Secondly, the maximum number of left or right otoliths, and the maximum number of upper or lower beaks, per sample, were counted. The latter provided an estimate of the minimum number of prey items. Damaged or eroded otoliths of a given species, that could not be divided into left or right, were divided by two.

Percentage of total mass for each prey item was calculated for all stomachs, including those with only trace remains. The mean mass for each individual species was multiplied by the minimum number of prey items.

Interviews with experienced local fishermen

Further information on the diet of seals was obtained from interviews conducted with experienced local fishermen at Plettenberg Bay.

Satellite telemetry

SLTDR

Wildlife computers microprocessor-controlled satellite-linked-time-depth-recorders (SLTDR) type 3 were used in this study. The type 3 software provides both at-sea and on-land locations through the Service Argos system, and the type 3 recorders transmit information on dive depths and duration. The SLTDRs were pre-programmed to sample depth every 10 seconds to determine dive duration and maximum depths.

Deployment of SLTDR

SLTDRs were attached to two female Cape fur seals at Black Rocks, Algoa Bay. The females selected for study were lactating (observed with a healthy pup) and had finished moulting.

The females were caught in a specially designed hoop net, and then strapped onto a harness board, and given 7 ml of valium. A section of the hoop net was untied, exposing the upper back of the animal. A patch of fur immediately behind the shoulders (along the mid-line) was washed with acetone to remove any oil, and then dried with paper towel. Devcon Plastic Welder-TM or Devcon 5-minute epoxy 14270 was massaged into the fur with a spatula, and was also smoothed over the base of the SLTDR. The SLTDR was placed firmly in position, with the aerial facing towards the head of the animal. The adhesive was smoothed up the side of the SLTDR. Tape was removed from the pressure transducer and the conductivity sensors, and cleaned with alcohol. The communication port was filled with silicon and covered with adhesive. Each seal was measured (SBL), and tagged in the left and right fore flippers before release.

SLTDR 15990 was deployed on March 19, 1993 attached to a 160 cm female tagged P6962 and P6963. SLTDR 15989 was deployed on September 15, 1994, attached to a 143 cm female tagged P6970 and P6971.

When decoding the dive depth and duration data, only messages which complied with all checks were included in analysis. When each of the checks (seven data bytes) were summed, the message was considered to be valid only if the sum was evenly divisible by 256. If not, the message may have been corrupted during reception and was subsequently discarded. Location data was classed from 0–3 (where 3 is best). When decoding location data, only locations classed as 1–3 were included in analysis. Statistical analysis and graphics were implemented in Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997).

RESULTS

Rodeklippe, Plettenberg Bay (non-breeding colony)

General composition of diet

Identifiable prey items were found in 98.5% of faecal samples collected at Rondeklippe colony. A total of 1 172 prey items were retrieved, including teleost fish (93.8%), cephalopods (3.9%), crustaceans (0.9%), and miscellaneous items (1.5%) (Table 9.5).

Fish otoliths occurred in 61 (95.3%) faecal samples. A total of 25 species of fish and 15 families were identified. Sixty one (5.6%) individual otoliths were broken or severely eroded and therefore could not be identified.

When all otoliths (n = 1 099) were examined, the most numerous fish species were *Cynoglossus zanzibarensis/capensis* (35% of otoliths), *Austroglossus pectoralis* (24% of otoliths), *Trachurus trachurus capensis* (10% of otoliths) and *Sardinops ocellatus* (10% of otoliths). A similar trend was observed when the maximum number of right or left otoliths in each sample was examined (n = 701), i.e., *C. zanzibarensis/capensis* (30% of otoliths), *A. pectoralis* (22% of otoliths), *S. ocellatus* (11% of otoliths) and *T. trachurus capensis* (10% of otoliths). The most frequently occurring fish species were *C. zanzibarensis/capensis* (in 58% of samples), *A. pectoralis* (in 55% of samples), *S. ocellatus* (in 30% of samples), *T. trachurus capensis* (in 28% of samples) and *Liza richardsonii* (in 23% of samples).

Cephalopod beaks occurred in 30 (46.9%) faecal samples (Table 9.5). A total of four species and three families were identified. Seven (15%) upper squid beaks were broken and therefore could not be identified. The most numerous and frequently occurring cephalopod species was *Loligo vulgaris reynaudii* (a minimum of 23 individuals in seven samples). *Todaropsis eblanae*, *Octopus magnificus* and *Octopus vulgaris* occurred infrequently.

Crustacean remains (10 items) occurred in 10 (15.6%) faecal samples (Table 9.5). The remains of one whole amphipod, and the claws and carapace fragments of at least nine decapods were recovered.

Miscellaneous dietary items included nine egg cases from a dogfish shark, *Squalus* sp. (in one sample); seaweed (in three samples); and fragments of unidentified molluscs (in five samples) (Table 9.5).

Reconstituted length and mass of individual prey species are presented in Table 9.6. The mean reconstituted fish prey mass and total length was 68 g and 177 mm, respectively. The mean reconstituted cephalopod prey mass and dorsal mantle length was 253 g and 191 mm, respectively.

Table 9.5 *The composition of prey species, by number and frequency, occurring in faecal samples from Cape fur seals collected at Rondeklippe colony, Plettenberg Bay, between June 1993 and November 1995*

Prey taxon	**Number of prey items**				**Frequency of occurrence**		**Prey habitat**
	N^a	**% N^a**	**N^b**	**% N^b**	**F**	**% F**	
TELEOST FISH							
Callanthiidae							
1. *Callanthias legras*	4	0.34	3	0.39	1	1.56	Benthic
Carangidae							
2. *Trachurus trachurus capensis*	114	9.73	67	8.77	18	28.13	Pelagic-midwater
Cheilodactylidae	1	0.09	1	0.13	1	1.56	Benthic
Clupeidae							
3. *Sardinops ocellatus*	112	9.56	77	10.08	19	29.69	Pelagic
Coracinidae							
4. *Coracinus capensis*	1	0.09	1	0.13	1	1.56	Benthic
Cynoglossidae							
5.*Cynoglossus zanzibarensis/ C. capensis*	383	32.68	213	27.88	37	57.81	Benthic
Engraulidae							
6. *Engraulis japonicus*	14	1.19	11	1.44	5	7.81	Pelagic
Haemulidae							
7. *Pomadasys commersonnii*	1	0.09	1	0.13	1	1.56	Benthic
8. *Pomodasys olivaceum*	12	1.02	7	0.92	1	1.56	Benthic
Merlucciidae							
9. *Merluccius capensis/ M. paradoxus*	35	2.99	29	3.80	11	17.19	Benthic
Monodactylidae							
10. *Monodactylus falciformis*	2	0.17	1	0.13	1	1.56	Bentho-pelagic
Mugilidae							
11. *Liza dumerilii*	1	0.09	1	0.13	1	1.56	Benthic
12. *Liza richardsonii*	24	2.05	21	2.75	15	23.44	Benthic
13. *Mugil cephalus*	3	0.26	3	0.39	2	3.13	Benthic
Pomatomidae							
14. *Pomatomus saltrix*	8	0.68	8	1.05	2	3.13	Benthic-midwater
Sciaenidae							
15. *Argyrosomus thorpei*	1	0.09	1	0.13	1	1.56	Benthic
16. *Umbrina canariensis*	2	0.17	2	0.26	2	3.13	Benthic
Soleidae							
17. *Austroglossus pectoralis*	262	22.35	152	19.90	35	54.69	Benthic
Sparidae							
18. *Argyrozona argyrozona*	1	0.09	1	0.13	1	1.56	Benthic
19. *Diplodus sargus capensis*	5	0.43	5	0.65	3	4.69	Benthic
20. *Lithognathus mormyrus*	48	4.10	31	4.06	9	14.06	Benthic
21. *Pagellus belottii natalensis*	2	0.17	2	0.26	2	3.13	Benthic
22. *Rhabdosargus sarba*	1	0.09	1	0.13	1	1.56	Benthic
23. *Sarpa salpa*	1	0.09	1	0.13	1	1.56	Benthic
Unidentified otoliths	61	5.20	61	7.98	23	35.94	
	1099	**93.81**	**701**	**91.75**	**194**		
CEPHALOPODS							
Loliginidae							
24. *Loligo vulgaris reynaudii*	31	2.65	23	3.01	7	10.94	Pelagic
Ommastrephidae							
25. *Todaropsis eblanae*	6	0.51	4	0.52	1	1.56	Pelagic
Unidentified squid	7	0.60	7	0.92	6	9.38	Pelagic
Octopodidae							
26. *Octopus magnificus*	1	0.09	1	0.13	1	1.56	Benthic
27. *Octopus vulgaris*	1	0.09	1	0.13	1	1.56	Benthic
	46	**3.94**	**36**	**4.71**	**16**		
CRUSTACEA							
Decapoda	9	0.77	9	1.18	9	14.06	
Amphipoda	1	0.09	1	0.13	1	1.56	
	10	**0.86**	**10**	**1.31**	**10**		
OTHER							
Dogfish shark egg cases (*Squalus sp.*)	9	0.77	9	1.18	1	1.56	
Unidentified molluscs	5	0.43	5	0.65	5	7.81	
Seaweed	3	0.26	3	0.39	3	4.69	
	17	**1.46**	**17**	**2.22**	**9**		
	1172	**100**	**764**	**100**	**64**		

1. goldie; 2. maasbanker; 3. South African pilchard; 4. galijoen; 5. redspotted tonguefish/sand tonguefish; 6. Cape anchovy; 7. spotted grunter; 8. piggy; 9. shallow-water hake/deep-water hake; 10. Cape moony; 11. groovy mullet; 12. southern mullet; 13. flathead mullet; 14. elf; 15. squaretail kob; 16. baardman; 17. east coast sole; 18. carpenter; 19. blacktail; 20. sand steenbras; 21. red tjor-tjor; 22. Natal stumpnose; 23 strepie; 24. chokker squid; 25. lesser flying squid; 26. giant octopus; and 27. common octopus.

N^a, total number of left and right otoliths per sample, or total number of upper and lower cephalopod beaks per sample.

N^b, minimum number of prey items present (maximum number of either right or left otoliths per sample, or maximum number of either upper or lower cephalopod beaks per sample).

F, frequency of occurrence (number of prey items per sample, *n* = 64 samples).

Table 9.6 *Mean length and mean mass of prey species occurring in faecal samples from Cape fur seals collected at Rondeklippe colony, Plettenberg Bay, between June 1993 and November 1995*

	Otolith or cephalopod beak			Prey species	
Prey taxon	**Mean length ± SE (mm)**	**Range (mm)**	***n***	**Mean length ± SE (mm)**	**Mean mass ± SE (g)**
TELEOST FISH					
Callanthiidae					
1. *Callanthias legras*	7.48 ± 0.19	7.19–7.97	4	–[a]	–[a]
Carangidae					
2. *Trachurus trachurus capensis*	5.94 ± 0.11	3.34–10.28	91	190.45 ± 3.68	67.79 ± 5.14
Cheilodactylidae	12.85	–	1	–[a]	–[a]
Clupeidae					
3. *Sardinops ocellatus*	3.98 ± 0.10	2.69–9.30	82	217.60 ± 6.12	108.20 ± 23.29
Coracinidae					
4. *Coracinus capensis*	13.1	–	1	–[a]	–[a]
Cynoglossidae					
5. *Cynoglossus zanzibarensis* (*C. capensis*)	3.69 ± 0.04	1.79–6.04	379	196.19 ± 2.51 (120.99 ± 0.53)	197.35 ± 23.56 (32.28 ± 1.34)
Engraulidae					
6. *Engraulis japonicus*	3.37 ± 0.07	2.95–3.73	14	99.52 ± 0.16	11.73 ± 0.65
Haemulidae					
7. *Pomadasys commersonnii*	9.00	–	1	218.70	105.53
8. *Pomodasys olivaceum*	7.17 ± 0.38	5.14–9.77	12	142.61 ± 8.47	45.49 ± 8.27
Merlucciidae					
9. *Merluccius capensis* (*M. paradoxus*)	7.51 ± 0.30	4.4–11.4	30	159.07 ± 7.29 (165.26 ± 8.06)	33.85 ± 5.09 (33.80 ± 5.57)
Monodactylidae					
10. *Monodactylus falciformis*	7.58 ± 0.9	5.78–7.58	2	181.58 ± 28.91	122.15 ± 54.94
Mugilidae					
11. *Liza dumerilii*	NR	–	0	–	–
12. *Liza richardsonii*	8.42 ± 0.31	6.04–10.92	20	306.66 ± 14.99	306.98 ± 41.94
13. *Mugil cephalus*	9.01 ± 1.16	6.9–10.92	3	396.23 ± 7.13	593.24 ± 32.74
Pomatomidae					
14. *Pomatomus saltrix*	NR	–	0	–	–
Sciaenidae					
15. *Argyrosomus thorpei*	NR	–	0	–	–
16. *Umbrina canariensis*	8.21 ± 1.31	6.90–9.51	2	197.71 ± 38.26	118.02 ± 64.14
Soleidae					
17. *Austroglossus pectoralis*	3.65 ± 0.04	1.67–7.08	259	237.58 ± 3.10	83.67 ± 4.1
Sparidae					
18. *Argyrozona argyrozona*	6.29	–	1	134.49	34.20
19. *Diplodus sargus capensis*	7.14 ± 0.51	5.78–7.97	4	250.07 ± 22.94	276.61 ± 67.01
20. *Lithognathus mormyrus*	5.52 ± 0.13	3.98–9.51	47	157.24 ± 5.65	69.19 ± 13.51
21. *Pagellus belottii natalensis*	7.71 ± 0.13	7.58–7.84	2	179.35 ± 3.17	76.53 ± 4.19
22. *Rhabdosargus sarba*	8.61	–	1	293.15	388.75
23. *Sarpa salpa*	5.65	–	1	195.00	107.49
	4.35 ± 0.05	**1.67–13.1**	**957**	**176.77 ± 2.16**	**67.53 ± 3.29**
CEPHALOPODS					
Loliginidae					
24. *Loligo vulgaris reynaudii*	3.54 ± 0.14[b]	2.31–4.70	14	220.21 ± 11.07	269.92 ± 32.46
Ommastrephidae					
25. *Todaropsis eblanae*	1.55 ± 0.05[b]	1.50–1.60	2	48.23 ± 1.73	7.36 ± 0.71
Octopodidae					
26. *Octopus magnificus*	15.9[c]	–	1	158.35	468.49
27. *Octopus vulgaris*	10.2[c]	–	1	97.64	290.98
	4.38 ± 0.80	**1.5–15.9**	**18**	**190.85 ± 16.65**	**252.95 ± 34.51**

[a] No regression available.

[b] Lower rostral length.

[c] Crest length.

NR, otolith length not recorded because the otolith was broken or eroded.
Mean length and mean mass for all fish combined was calculated using *Cynoglossus zanzibarensis* and *Merluccius capensis*.
Reconstituted length is dorsal mantle length for cephalopods and total length for fish.
Common names for fish and cephalopods given in Table 9.5.

Black Rocks, Algoa Bay (breeding colony)

General composition of diet

Identifiable prey items were found in all faecal samples/regurgitates collected at Black Rocks. A total of 1 483 prey items were retrieved including teleost fish (41.3%), cephalopods (57.3%), crustaceans (1.2%), and miscellaneous items (0.2%) (Table 9.7).

Fish otoliths occurred in 12 (92.3%) faecal samples/regurgitates. A total of 24 species of fish and 13 families were identified. Fifty two (8.5%) individual otoliths were broken or severely eroded and therefore could not be identified. Three otoliths were classified to family level only – two Mugilidae and one Sparidae.

Table 9.7 ***The composition of prey species, by number and frequency, occurring in faecal samples and regurgitates from Cape fur seals collected at Black Rocks seal colony, Algoa Bay, between May 1992 and November 1995***

Prey taxon	**Number of prey items**				**Frequency of occurrence**		**Prey habitat**
	N^a	**% N^a**	**N^b**	**% N^b**	**F**	**% F**	
TELEOST FISH							
Carangidae							
1. *Trachurus trachurus capensis*	115	7.75	64	7.32	10	76.92	Pelagic-midwater
Clupeidae							
2. *Sardinops ocellatus*	68	4.59	42	4.81	9	69.23	Pelagic
Cynoglossidae							
3. *Cynoglossus zanzibarensis*/ *C. capensis*	40	2.70	22	2.51	7	53.85	Benthic
Engraulidae							
4. *Engraulis japonicus*	111	7.48	63	7.21	7	53.85	Pelagic
Haemulidae							
5. *Pomodasys olivaceum*	1	0.07	1	0.11	1	7.69	Benthic
Merlucciidae							
6. *Merluccius capensis*/ *M. paradoxus*	49	3.30	35	4.00	10	76.92	Benthic
Mugilidae							
7. *Mugil cephalus*	2	0.13	2	0.23	1	7.69	Benthic
Unidentified Mugilidae	2	0.13	2	0.23	1	7.69	Benthic
Ophidiidae							
8. *Genypterus capensis*	16	1.08	13	1.49	4	30.77	Benthic
Sciaenidae							
9. *Argyrosomus hololepidotus*	11	0.74	10	1.14	5	38.46	Benthic
10.*Umbrina canariensis*	14	0.94	9	1.03	6	46.15	Benthic
Scorpaenidae							
11. *Helicolenus dactylopterus*	5	0.34	3	0.34	2	15.38	Benthic
Soleidae							
12. *Austroglossus pectoralis*	23	1.55	14	1.60	8	61.54	Benthic
Sparidae							
13. *Argyrozona argyrozona*	2	0.13	2	0.23	1	7.69	Benthic
14. *Boopsoidae inornata*	1	0.07	1	0.11	1	7.69	Benthic
15. *Chrysoblephus cristiceps*	1	0.07	1	0.11	1	7.69	Benthic
16. *Diplodus sargus capensis*	2	0.13	1	0.11	1	7.69	Benthic
17. *Lithognathus mormyrus*	3	0.20	3	0.34	2	15.38	Benthic
18. P*agellus belottii natalensis*	85	5.73	47	5.38	8	61.54	Benthic
19. *Rhabdosargus holubi*	8	0.54	8	0.92	6	46.15	Benthic
Unidentified Sparidae	1	0.07	1	0.11	1	7.69	Benthic
Trichiuridae							
20. *Lepidopus caudatus*	1	0.07	1	0.11	1	7.69	Bentho-pelagic
Unidentified otoliths	52	3.51	27	3.09	7	53.85	
	613	**41.34**	**372**	**42.56**	**100**		
CEPHALOPODS							
Loliginidae							
21. *Loligo vulgaris reynaudii*	836	56.37	470	53.78	13	100	Pelagic
Ommastrephidae							
22. *Todaropsis eblanae*	1	0.07	1	0.11	1	7.69	Pelagic
Unidentified squid	4	0.27	2	0.23	1	7.69	Pelagic
Octopodidae							
23. *Octopus vulgaris*	7	0.47	7	0.80	5	38.46	Benthic
Sepiidae							
24. *Sepia* sp.	1	0.07	1	0.11	1	7.69	Benthic
	849	**57.25**	**481**	**55.03**	**21**		
CRUSTACEA							
Decapoda	18	1.21	18	2.06	7	53.85	
	18	**1.21**	**18**	**2.06**	**7**		
OTHER							
Dogfish shark egg cases (*Squalus* sp.)	2	0.13	2	0.23	1	7.69	
Penguin feathers	1*	0.07	1*	0.11	1	7.69	
	3	**0.20**	**3**	**0.34**	**2**		
	1483	**100**	**874**	**100**	**13**		

1. maasbanker; 2. South African pilchard; 3. redspotted tonguefish/sand tonguefish; 4. Cape anchovy; 5. piggy; 6. shallow-water hake/deep-water hake; 7. flathead mullet; 8. kingklip; 9. kob; 10. baardman; 11. jacopever; 12. east coast sole; 13. carpenter; 14. fransmadam; 15. dageraad; 16. blacktail; 17. sand steenbras; 18. red tjor-tjor; 19. Cape stumpnose; 20. buttersnoek; 21. chokker squid; 22. lesser flying squid; 23. common octopus; and 24. cuttlefish.

N^a, total number of left and right otoliths per sample, or total number of upper and lower cephalopod beaks per sample.

N^b, minimum number of prey items present (maximum number of either right or left otoliths per sample, or maximum number of either upper or lower cephalopod beaks per sample).

F, frequency of occurrence (number of prey items per sample; $n = 13$ samples).

* Five feathers presumably from one penguin.

When all otoliths (*n* = 613) were examined, the most numerous fish species were *T. trachurus capensis* (19% of otoliths), *Engraulis japonicus* (18% of otoliths), *Pagellus bellottii natalensis* (14% of otoliths) and *S. ocellatus* (11% of otoliths). A similar trend was observed when the maximum number of right or left otoliths in each sample was examined (*n* = 372), i.e., *T. trachurus capensis* (17% of otoliths), *E. japonicus* (17% of otoliths), *P. bellottii natalensis* (13% of otoliths) and *S. ocellatus* (11% of otoliths). The most frequently occurring fish species were *T. trachurus capensis* (in 77% of samples), *Merluccius capensis/paradoxus* (in 77% of samples), *S. ocellatus* (in 69% of samples), *P. bellottii natalensis* (in 62% of samples) and *A. pectoralis* (in 62% of samples).

Cephalopod beaks occurred in all faecal samples/regurgitates (Table 9.7). A total of three species of cephalopods and four families were identified (Table 9.6). Two upper and two lower beaks (0.5%) were broken and therefore could not be identified. One cuttlefish was identified to genus level only - *Sepia* sp. The most numerous and frequently occurring cephalopod species was

Table 9.8 ***Mean length and mean mass of prey species occurring in faecal samples and regurgitates from Cape fur seals collected at Black Rocks seal colony, Algoa Bay, between May 1992 and November 1995***

	Otolith or cephalopod beak			**Prey species**	
Prey taxon	**Mean length ± SE (mm)**	**Range (mm)**	***n***	**Mean length ± SE (mm)**	**Mean mass ± SE (g)**
TELEOST FISH					
Carangidae					
1. *Trachurus trachurus capensis*	9.49 ± 0.52	6.50–12.80	46	313.18 ± 8.34	299.07 ± 23.81
Clupeidae					
2. *Sardinops ocellatus*	3.73 ± 0.07	2.57–5.14	53	214.11 ± 4.06	82.65 ± 4.90
Cynoglossidae					
3. *Cynoglossus zanzibarensis*	4.36 ± 0.15	1.79–6.04	38	240.92 ± 10.01	89.79 ± 9.15
(C. capensis)				(203.48 ± 9.07)	(64.20 ± 7.48)
Engraulidae					
4. *Engraulis japonicus*	3.68 ± 0.5	2.96–6.29	95	133.31 ± 1.49	15.47 ± 0.70
Haemulidae					
5. *Pomodasys olivaceum*	7.40	–	1	147.33	44.84
Merlucciidae					
6. *Merluccius capensis*	12.58 ± 0.92	7.30–21.30	18	286.49 ± 23.97	251.04 ± 68.22
(M. paradoxus)				(309.33 ± 27.57)	(307.08 ± 90.86)
Mugilidae					
7. *Mugil cephalus*	9.40	–	2	418.32	592.14
Ophidiidae					
8. *Genypterus capensis*	12.09 ± 2.37	8.90–15.20	7	545.93 ± 61.63	968.42 ± 303.60
Sciaenidae					
9. *Argyrosomus hololepidotus*	12.07 ± 0.45	10.20–14.20	6	339.23 ± 22.65	377.70 ± 75.31
10. *Umbrina canariensis*	9.38 ± 0.37	7.30–12.30	14	232.61 ± 2.93	192.41 ± 10.72
Scorpaenidae					
11. *Helicolenus dactylopterus*	11.10 ± 0.30	10.80–11.40	2	289.76 ± 0.82	398.23 ± 3.09
Soleidae					
12. *Austroglossus pectoralis*	4.49 ± 0.15	3.08–5.78	21	302.03 ± 11.65	172.85 ± 21.10
Sparidae					
13. *Argyrozona argyrozona*	12.45	11.70–13.20	2	313.44 ± 23.35	372.69 ± 77.00
14. *Boopsoidae inornata*	NR	–	0		
15. *Chrysoblephus cristiceps*	NR	–	0		
16. *Diplodus sargus capensis*	7.40 ± 0.70	6.70–8.10	2	261.68 ± 32.24	309.11 ± 111.57
17. *Lithognathus mormyrus*	8.97 ± 0.20	8.60–9.30	3	315.71 ± 1.01	500.86 ± 3.93
18. *Pagellus belottii natalensis*	8.23 ± 0.10	4.90–10.30	84	192.12 ± 2.56	99.13 ± 3.90
19. *Rhabdosargus holubi*	11.10 ± 0.83	9.00–13.50	6	371.13 ± 33.67	946.43 ± 244.71
Trichiuridae					
20. L*epidopus caudatus*	12.0	–	1	–	–
	6.59 ± 0.16	**1.79–21.30**	**401**	**225.53 ± 4.60**	**154.51 ± 11.87**
CEPHALOPODS					
Loliginidae					
21. *Loligo vulgaris reynaudii*	3.73 ± 0.55[a]	1.9–4.9	321	232.65 ± 2.13	308.42 ± 6.48
Ommastrephidae					
22. *Todaropsis eblanae*	2.1[a]	–	1	67.76	18.20
Octopodidae					
23. O*ctopus vulgaris*	10.34 ± 1.44[b]	7.9–15.2	5	74.76 ± 1.48	155.79 ± 6.73
Sepiidae					
24. *Sepia* sp.	NR	–	0	–	–
	3.83 ± 0.06	**1.90–15.20**	**327**	**229.73 ± 2.40**	**305.20 ± 6.51**

[a] Lower rostral length.

[b] Crest length.

NR, otolith length not recorded because the otolith was broken or eroded.

Mean length and mean mass for all fish combined was calculated using *Cynoglossus zanzibarensis* and *Merluccius capensis.*

Reconstituted length is dorsal mantle length for cephalopods and total length for fish.

Common names for fish and cephalopods are given in Table 9.7.

L. vulgaris reynaudii (a minimum of 470 individuals in 13 samples) followed by *O. vulgaris* (a minimum of seven individuals in five samples). *Todaropsis eblanae* and *Sepia* sp. occurred infrequently.

Crustacean remains (18 items) occurred in seven (54%) samples (Table 9.7). The claws and carapace fragments of at least 18 decapods were recovered.

Miscellaneous items included two egg cases from a dogfish shark, *Squalus* sp. (in one sample); and five feathers from an African penguin, *Spheniscus demersus* (in one sample) (Table 9.7).

Reconstituted length and mass of individual prey species are presented in Table 9.8. The mean reconstituted fish prey mass and total length was 155 g and 226 mm, respectively. The mean reconstituted cephalopod prey mass and dorsal mantle length was 305 g and 230 mm, respectively.

Cape fur seals stranded along the Eastern Cape coast

General composition of diet

Forty one stomachs collected from stranded (dead) seals along the Eastern Cape coast between January 1991 and December 1995 were examined. Twenty one stomachs (51%) contained identifiable remains (Table 9.9). The remanding 20 stomachs were empty. A total of 329 prey items were retrieved, including

Table 9.9 ***The composition of prey species, by number and frequency, occurring in the stomachs of Cape fur seals stranded off the Eastern Cape coast between January 1991 and December 1995***

	Number of prey items				**Frequency of occurrence**		**Prey habitat**
Prey taxon	**N^a**	**% N^a**	**N^b**	**% N^b**	**F**	**% F**	
TELEOST FISH							
Carangidae							
1. *Trachurus trachurus capensis*	54	16.41	29	14.50	4	9.76	Pelagic-midwater
Clupeidae							
2. *Etrumeus whiteheadi*	38	11.55	22	11.00	2	4.88	Pelagic
3. *Sardinops ocellatus*	7	2.13	4	2.00	2	4.88	Pelagic
Cynoglossidae							
4. *Cynoglossus zanzibarensis/ C. capensis*	24	7.30	13	6.50	3	7.32	Benthic
Merlucciidae							
5. *Merluccius capensis/ M. paradoxus*	17	5.17	9	4.50	3	7.32	Benthic
Ophidiidae							
6. *Genypterus capensis*	1	0.30	1	0.50	1	2.44	Benthic
Scorpaenidae							
7. *Helicolenus dactylopterus*	4	1.22	3	1.50	2	4.88	Benthic
Soleidae							
8. *Austroglossus pectoralis*	2	0.61	1	0.50	1	2.44	Benthic
Sparidae							
9. *Argyrozona argyrozona*	6	1.82	4	2.00	1	2.44	Benthic
10. *Pagellus belottii natalensis*	45	13.68	24	12.00	1	2.44	Benthic
11. *Pterogymnus laniaris*	1	0.30	1	0.50	1	2.44	Benthic
12. *Rhabdosargus sarba*	2	0.61	1	0.50	1	2.44	Benthic
Unidentified otoliths	6	1.82	3	1.50	2	4.88	
	207	**62.92**	**115**	**57.50**	**24**		
CEPHALOPODS							
Loliginidae							
13. *Loligo vulgaris reynaudii*	77	23.40	42	21.0	8	19.51	Pelagic
Octopodidae							
14. *Octopus vulgaris*	1	0.30	1	0.50	1	2.44	Benthic
Unidentified octopus	6	1.82	4	2.0	4	9.76	Benthic
	84	**25.53**	**47**	**23.50**	**13**		
CRUSTACEA							
Decapoda	2	0.61	2	1.00	1	2.44	
Amphipoda	20	6.08	20	10.00	1	2.44	
	22	**6.69**	**22**	**11.00**	**2**		
OTHER							
Dogfish shark egg case (*Squalus* sp.)	1	0.30	1	0.50	1	2.44	
Stones	15	4.56	15	7.46	2	4.88	
	16	**4.86**	**16**	**8.00**	**3**		
	329	**100**	**200**	**100**	**41**		

1. maasbanker; 2. redeye roundherring; 3. South African pilchard; 4. redspotted tonguefish/ sand tonguefish; 5. shallow-water hake/deep-water hake; 6. kingklip; 7. jacopever; 8. east coast sole; 9. carpenter; 10. red tjor-tjor; 11. panga; 12. Natal stumpnose; 13. chokker squid; and 14. common octopus.

N^a, total number of left and right otoliths per sample, or total number of upper and lower cephalopod beaks per sample.

N^b, minimum number of prey items present (maximum number of either right or left otoliths per sample, or maximum number of either upper or lower cephalopod beaks per sample).

F, frequency of occurrence (number of prey items per sample, *n* = 41 stomachs).

teleost fish (63%), cephalopods (26%), crustaceans (7%), and miscellaneous items (5%) (Table 9.8).

Fish otoliths occurred in 10 (48%) stomachs. A total of 14 species of fish and eight families were identified. Six (2.9%) individual otoliths could not be identified.

When all otoliths (*n* = 207) were examined, the most numerous fish species were *T. trachurus capensis* (26% of otoliths), *P. bellottii natalensis* (22% of otoliths), *Etrumeus whiteheadi* (18% of otoliths), *C. zanzibarensis/capensis* (12% of otoliths) and *M. capensis/paradoxus* (8% of otoliths). A similar trend was observed when the maximum number of right or left otoliths in each sample was examined (*n* = 115), i.e., *T. trachurus capensis* (25% of otoliths), *P. bellottii natalensis* (21% of otoliths), *E. whiteheadi* (19% of otoliths), *C. zanzibarensis/capensis* (11% of otoliths) and *M. capensis/paradoxus* (8% of otoliths). The most frequently occurring fish species were *T. trachurus capensis* (in 10% of stomachs), *C. zanzibarensis/capensis* (in 7% of stomachs) and *M. capensis/paradoxus* (in 7% of stomachs).

Cephalopod beaks occurred in 12 (57%) stomachs (Table 9.9). A total of two species and two families were identified. Four lower and two upper (7%) octopus beaks could not be identified. The most numerous and frequently occurring cephalopod species was *L. vulgaris reynaudii* (a minimum of 42 individuals in eight stomachs). A minimum of four unidentified octopus species occurred in four stomachs. *O. vulgaris* occurred infrequently.

Crustacean remains (22 items) occurred in two (9.5%) stomachs (Table 9.9). The remains of 20 whole amphipods, and the claws and carapace fragments of at least two decapods were recovered.

Miscellaneous dietary items included one egg case from a dogfish shark, *Squalus* sp. (in one stomach); and 15 stones (in two stomachs) (Table 9.9). One young male (PEM2198, 105 cm SBL) had 13 stones in its stomach which weighed 34.3 g. A second animal, an old male (PEM2203, 204 cm SBL) had two stones in its stomach which weighed 40.4 g. Mean mass of the 15 stones was 5.1 ± 1.8 g (range 0.1–25.0 g); mean length was 18.3 ± 2.3 mm (range

Table 9.10 ***Mean length and mean mass of prey species occurring in the stomachs of Cape fur seals stranded off the Eastern Cape coast between January 1991 and December 1995***

Prey taxon	**Otolith or cephalopod beak**			**Prey species**			
	Mean length ± SE (mm)	**Range (mm)**	***n***	**Mean length ± SE (mm)**	**Mean mass ± SE (g)**	**Total mass (g)**	**%Total mass**
TELEOST FISH							
Carangidae							
1. *Trachurus trachurus capensis*	8.91 ± 0.37	7.00–12.21	23	293.13 ± 12.82	252.89 ± 34.43	7333	27.59
Clupeidae							
2. *Etrumeus whiteheadi*	3.96 ± 0.06	3.3–4.4	23	205.13 ± 3.55	65.89 ± 3.51	1450	4.14
3. *Sardinops ocellatus*	3.92 ± 0.06	3.86–3.98	2	225.55 ± 3.69	91.69 ± 4.76	367	0.19
Cynoglossidae							
4. *Cynoglossus zanzibarensis*	5.03 ± 0.17	2.27–6.43	23	286.51 ± 11.75	138.93 ± 13.47	1806	3.05
(C. capensis)				(245.28 ± 10.76)	(105.16 ± 11.65)	(1367)	
Merlucciidae							
5. *Merluccius capensis*	10.56 ± 0.34	9.20–11.80	8	233.61 ± 8.58	95.41 ± 10.84	859	1.00
(M. paradoxus)				(248.19 ± 9.68)	(102.30 ± 12.65)	(921)	
Ophidiidae							
6. *Genypterus capensis*	11.3	–	1	484.43	501.70	502	0.07
Scorpaenidae							
7. *Helicolenus dactylopterus*	9.98 ± 0.96	7.10–11.20	4	254.99 ± 29.58	298.99 ± 77.17	897	0.30
Soleidae							
8. *Austroglossus pectoralis*	4.11	–	2	272.13	111.57	112	0.01
Sparidae							
9. *Argyrozona argyrozona*	13.38 ± 0.35	12.90–14.40	4	328.30 ±16.46	402.27 ± 80.63	1609	0.84
10. *Pagellus belottii natalensis*	8.59 ± 0.31	7.19–10.15	24	200.96 ± 4.46	112.88 ± 7.86	2709	8.44
11. *Pterogymnus laniaris*	8.4	–	1	185.99	105.10	105	0.01
12. *Rhabdosargus sarba*	10.4	–	1	925.25	384.19	384	0.05
	7.26 ± 0.26	**2.27–14.40**	**116**	**251.56 ± 5.97**	**164.09 ± 13.76**	**352494**	**45.73**
CEPHALOPODS							
Loliginidae							
13. *Loligo vulgaris reynaudii*	3.42 ± 0.06[a]	2.60–4.30	38	210.68 ± 4.47	237.06 ± 12.23	418174	54.25
Octopodidae							
14. *Octopus vulgaris*	6.7[b]	–	1	60.57	105.15	105	0.01
Unidentified octopus	17.00 ± 1.50	15.50–18.50	2	–	–	–	–
	4.16 ± 0.47	**2.60–18.50**	**41**	**206.64 ± 5.81**	**233.67 ± 12.38**	**418279**	**54.27**

[a] Lower rostral length.

[b] Crest length.

Mean length and mean mass for all fish combined was calculated using *Cynoglossus zanzibarensis* and *Merluccius capensis.*

Reconstituted length is dorsal mantle length for cephalopods and total length for fish.

Common names for fish and cephalopods are given in Table 9.9.

Total mass and % total mass was calculated from the minimum number of prey items present. Regression equations for *Cynoglossus zanzibarensis* and *Merluccius capensis* were used.

8.0–39.1 mm); and mean width was 13.1 ± 1.6 mm (range 4.3–23.7 mm).

Reconstituted length and mass of individual prey species are presented in Table 9.10. The mean reconstituted fish prey mass and total length was 164 g and 252 mm, respectively. The mean reconstituted cephalopod prey mass and dorsal mantle length was 234 g and 207 mm, respectively.

The most important prey species based on percent total mass were *L. vulgaris reynaudii* (54%), *T. trachurus capensis* (28%), *P. bellottii natalensis* (8%), *E. whiteheadi* (4%) and *C. zanzibarensis/ capensis* (3%) (Table 9.10).

An additional five stomachs from black pups (68–81 cm in length) were examined and analysed separately. Two of these stomachs contained milk (PEM2020, PEM2021); and one contained one small stone, one piece of seaweed and two molluscs (PEM2024). The remaining two stomachs were empty (PEM2022, PEM2025).

Cape fur seals incidentally entrapped in trawl nets during commercial fishing operations (by-catch) off the Eastern Cape coast

General composition of diet

Thirty seven stomachs collected from seals incidentally entrapped in trawl nets during commercial fishing operations off the Eastern Cape coast between July 1992 and August 1995 were examined. Thirty five stomachs (95%) contained identifiable remains (Table 9.11). The remanding two stomachs were empty. A total of 785 prey items were retrieved, including teleost fish (87%), cephalopods (10%), crustaceans (2%), and miscellaneous items (1%) (Table 9.11).

Fish otoliths occurred in 35 (95%) stomachs. A total of 17 species of fish and 15 families were identified. Eleven (1.6%) individual otoliths could not be identified.

When all otoliths (n = 684) were examined, the most numerous fish species were *M. capensis/ paradoxus* (41% of otoliths), *T. trachurus capensis* (33% of otoliths), *Helicolenus dactylopterus* (7% of otoliths) and *Scomber japonicus* (5% of otoliths). A similar trend was observed when the maximum number of right or left otoliths in each sample was examined (n = 378), i.e., *M. capensis/paradoxus* (41% of otoliths), *T. trachurus capensis* (32% of otoliths), and *H. dactylopterus* (7% of otoliths). The most frequently occurring fish species were *M. capensis/ paradoxus* (in 24% of stomachs), *T. trachurus capensis* (in 24% of stomachs) and *Lepidopus caudatus* (in 13% of stomachs).

Cephalopod beaks occurred in 24 (65%) stomachs (Table 9.11). A total of five species and four families were identified. Six lower and six upper (15%) octopus beaks could not be identified. The most numerous and frequently occurring cephalopod species were *L. vulgaris reynaudii* (a minimum of 17 individuals in six stomachs), *Lycoteuthis diadema* (a minimum of 10 individuals in six stomachs) and *O. magnificus* (a minimum of 7 individuals in four stomachs). A minimum of six unidentified octopus species occurred in four stomachs. *Todaropsis eblanae* and *Ommastrephes bartramii* occurred infrequently.

Crustacean remains (13 items) occurred in eight (22%) stomachs (Table 9.11). One whole mantis shrimp (stomatopoda), and the claws and carapace fragments of at least twelve decapods were recovered.

One male (PEM2258, 170 cm SBL) had eight stones in its stomach which weighed 34.3 g. Mean mass of the eight stones was 22.5 ± 7.3 g (range 0.8–54.5 g); mean length was 38.7 ± 6.9 mm (range 9.7–75.5 mm); and mean width was 25.4 ± 3.8 mm (range 9.5–41.3 mm).

Reconstituted length and mass of individual prey species are presented in Table 9.12. The mean reconstituted fish prey mass and total length was 1067 g and 363 mm, respectively. The mean reconstituted cephalopod prey mass and dorsal mantle length was 1 090 g and 184 mm, respectively.

The most important prey species based on percent total mass were *L. caudatus* (71%), *M. capensis/paradoxus* (9%), *T. trachurus capensis* (7%), and *O. magnificus* (6%) (Table 9.12).

Analysis based on the modified volume approach (David, 1991), which is a revised method for calculation of components of seal diet from stomachs which contain undigested prey remains, is presented elsewhere.

Table 9.11 *The composition of prey species, by number and frequency, occurring in the stomachs of Cape fur seals incidentally entrapped in trawl nets during commercial fishing operations off the Eastern Cape coast between July 1992 and August 1995*

Prey taxon	**Number of prey items**				**Frequency of occurrence**		**Prey habitat**
	N^a	**% N^a**	**N^b**	**% N^b**	**F**	**% F**	
TELEOST FISH							
Anguillidae							
1. *Gnathophis capensis*	10	1.27	7	1.58	2	5.41	Benthic
Carangidae							
2. *Trachurus trachurus capensis*	227	28.92	121	27.31	24	64.86	Pelagic-midwater
Clupeidae							
3. *Etrumeus whiteheadi*	12	1.53	6	1.35	2	5.41	Pelagic
4. *Sardinops ocellatus*	2	0.25	1	0.23	1	2.70	Pelagic
Cynoglossidae							
5. *Cynoglossus zanzibarensis/ C. capensis*	8	1.02	4	0.90	1	2.70	Benthic
Gonorhynchidae							
6. *Gonorhynchus gonorhynchus*	2	0.25	1	0.23	1	2.70	Benthic
Lophiidae							
7. *Lophiodes* sp.	2	0.25	1	0.23	1	2.70	Benthic
Merlucciidae							
8. *Merluccius capensis/ M. paradoxus*	283	36.05	155	34.99	24	64.86	Benthic
Myctophidae	5	0.64	3	0.68	1	2.70	
Sciaenidae							
9. *Umbrina canariensis*	2	0.25	1	0.23	1	2.70	Benthic
Scombridae							
10. *Scomber japonicus*	33	4.20	17	3.84	7	18.92	Epipelagic-demersal
Scorpaenidae							
11. *Helicolenus dactylopterus*	47	5.99	28	6.32	7	18.92	Benthic
Soleidae							
12. *Austroglossus pectoralis*	2	0.25	1	0.23	1	2.70	Benthic
Sparidae							
13. *Rhabdosargus sarba*	2	0.25	1	0.23	1	2.70	Benthic
Trichiuridae							
14. *Lepidopus caudatus*	30	3.82	22	4.97	13	35.14	Bentho-pelagic
Zeidae							
15. *Zeus faber*	6	0.76	3	0.68	1	2.70	Benthic
Unidentified otoliths	11	1.40	6	1.35	2	5.41	
	684	**87.13**	**378**	**85.33**	**90**		
CEPHALOPODS							
Loliginidae							
16. *Loligo vulgaris reynaudii*	32	4.08	17	3.84	6	16.22	Pelagic
Lycoteuthidae							
17. *Lycoteuthis diadema*	15	1.91	10	2.26	6	16.22	Pelagic
Ommastrephidae							
18. *Todaropsis eblanae*	5	0.64	3	0.68	2	5.41	Pelagic
19. *Ommastrephes bartramii*	2	0.25	1	0.23	1	2.70	Pelagic
Octopodidae							
20. *Octopus magnificus*	14	1.78	7	1.58	4	10.81	Benthic
Unidentified octopus	12	1.53	6	1.35	4	10.81	Pelagic
	80	**10.19**	**44**	**9.93**	**23**		
CRUSTACEA							
Decapoda	12	1.53	12	2.71	7	18.92	
Stomatopoda	1	0.13	1	0.23	1	2.70	
	13	**1.66**	**13**	**2.93**	**8**		
OTHER							
Stones	8	1.02	8	1.81	1	2.70	
	785	**100**	**443**	**100**	**37**		

1. southern conger; 2. maasbanker; 3. redeye roundherring; 4. South African pilchard; 5. redspotted tonguefish/sand tonguefish; 6. beaked sandfish; 7. monk fish; 8. shallow-water hake/deep-water hake; 9. baardman; 10. mackerel; 11. jacopever; 12. east coast sole; 13. Natal stumpnose; 14. buttersnoek; 15. John Dory; 16. chokker squid; 17. a squid; 18. lesser flying squid; 19. neon flying squid; and 20. giant octopus.

N^a, total number of left and right otoliths per sample, or total number of upper and lower cephalopod beaks per sample.

N^b, minimum number of prey items present (maximum number of either right or left otoliths per sample, or maximum number of either upper or lower cephalopod beaks per sample).

F, frequency of occurrence (number of prey items per sample, *n* = 37 stomachs).

Table 9.12 *Mean length and mean mass of prey species occurring in the stomachs of Cape fur seals incidentally entrapped in trawl nets during commercial fishing operations off the Eastern Cape coast between July 1992 and August 1995*

Prey taxon	**Otolith or cephalopod beak**			**Prey species**			
	Mean length ± SE (mm)	**Range (mm)**	***n***	**Mean length ± SE (mm)**	**Mean mass ± SE (g)**	**Total mass (g)**	**% Total mass**
TELEOST FISH							
Anguillidae							
1. *Gnathophis capensis*	8.18 ± 0.49	7.07–11.60	10	296.45 ± 29.21	137.89 ± 55.52	965	0.17
Carangidae							
2. *Trachurus trachurus capensis*	10.07 ± 9.70	6.43–18.35	65	333.55 ± 7.17	362.26 ± 34.03	43834	7.88
Clupeidae							
3. *Etrumeus whiteheadi*	4.13 ± 0.14	3.73–4.49	6	76.47 ± 8.84	235.51 ± 221.02	459	0.08
4. *Sardinops ocellatus*	4.2	–	1	242.81	115.79	116	0.02
Cynoglossidae							
5. *Cynoglossus zanzibarensis*	4.85 ± 0.48	3.86–6.04	4	136.16 ± 0.96	94.00 ± 5.24	8340	1.50
(C. capensis)				(274.07 ± 3.48)	(2085.02 ± 38.72)	(376)	
Gonorhynchidae							
6. *Gonorhynchus gonorhynchus*	4.55 ± 0.05	4.50–4.60	2	406.13 ± 4.50	331.23 ± 12.14	331	0.06
Lophiidae							
7. *Lophiodes sp.*	NR	–	–	–	–	–	–
Merlucciidae							
8. *Merluccius capensis*	14.27 ± 0.28	8.80–25.20	133	329.52 ± 7.56	340.82 ± 30.05	52827	9.50
(M. paradoxus)				(358.34 ± 8.79)	(423.35 ± 41.66)	(65619)	
Myctophidae	2.22 ± 0.11	1.93–2.44	4	–	–	–	–
Sciaenidae							
9. *Umbrina canariensis*	12.85 ± 1.00	12.80–12.90	2	340.84 ± 1.62	571.31 ± 8.44	571	0.10
Scombridae							
10. *Scomber japonicus*	5.59 ± 0.32	5.27–5.90	2	327.07 ± 8.94	473.92 ± 34.62	8057	1.45
Scorpaenidae							
11. *Helicolenus dactylopterus*	9.51 ± 0.22	7.70–11.10	24	239.67 ± 6.79	233.02 ± 19.33	6524	1.17
Soleidae							
12. *Austroglossus pectoralis*	NR	–	–	–	–		
Sparidae							
13. *Rhabdosargus sarba*	11.95 ± 0.05	11.90–12.00	2	468.75 ± 2.81	1751.08 ± 33.63	1751	0.31
Trichiuridae							
14. *Lepidopus caudatus*	8.15 ± 1.42	5.78–22.30	11	1431.46 ± 416.35	17900.33 ± 17039.26	393807	71
Zeidae							
15. *Zeus faber*	NR	–	–	–	–	–	–
	11.57 ± 0.25	**1.93–25.20**	**266**	**363.27 ± 21.11**	**1067.23 ± 681.52**	**583578**	**93.05**
CEPHALOPODS							
Loliginidae							
16. *Loligo vulgaris reynaudii*	3.39 ± 0.11[a]	2.50–4.30	15	208.80 ± 7.91	233.28 ± 21.93	3966	0.71
Lycoteuthidae							
17. *Lycoteuthis diadema*	3.52 ± 0.04[a]	3.30–3.70	9	99.94 ± 1.26	45.75 ± 1.66	458	0.08
Ommastrephidae							
18. *Todaropsis eblanae*	5.13 ± 0.43[a]	4.30–5.70	3	184.54 ± 17.04	274.02 ± 61.43	822	0.15
19. *Ommastrephes bartramii*	4.4[a]	–	1	174.18	134.41	134	0.02
Octopodidae							
20. *Octopus magnificus*	24.79 ± 2.29[b]	11.50–30.30	7	239.87 ± 20.99	4756.68 ± 1155.22	33297	5.99
	7.88 ± 1.52	**2.50–30.30**	**35**	**183.95 ± 10.38**	**1090.41 ± 382.41**	**38677**	**6.95**

[a] Lower rostral length.

[b] Crest length.

NR, otolith length not recorded because the otolith was broken or eroded.

Mean length and mean mass for all fish combined was calculated using *Cynoglossus zanzibarensis* and *Merluccius capensis*.

Reconstituted length is dorsal mantle length for cephalopods and total length for fish.

Common names for fish and cephalopods given in Table 9.11.

Total mass and % total mass was calculated from the minimum number of prey items present. Regression equations for *Cynoglossus zanzibarensis* and *Merluccius capensis* were used.

Table 9.13 *Size of commercially important prey items in the diet of the Cape fur seals from the Eastern Cape coast (Plettenberg Bay to Port Alfred)*

	Seal prey size			Size of the local commercial catch	
Species	**Mean ± SE (mm)**	**Mode (mm)**	***n***		
Trawl fishery				**Range (mm)**	
Merluccius capensis	294.30 ± 7.45	287.73	189	30–980	a
Merluccius paradoxus	318.36 ± 8.56	309.59		60–850	
Trachurus trachurus capensis	267.38 ± 5.43	184.82	225	60–560	a
Squid jig fishery				**Mode (mm)**	
Loligo vulgaris reynaudii	229.13 ± 1.92	229.96	388	290 males 180 females	b

(a) Species lengths derived from research surveys aboard inshore/offshore trawlers in Eastern Cape waters in 1997 (Chris Wilke, pers. comm).

(b) Augustyn & Smale, 1995.

Prey size and size of local commercial catches

Seal prey species which were: (i) the most abundant, (ii) occurred most frequently, and (iii) were also of importance to the local commercial fisheries, included *Trachurus trachurus capensis*, *Merluccius capensis/paradoxus* and *Loligo vulgaris reynaudii*. Modal prey size of these four species were within the size range of local commercial catches (Table 9.13). This indicates that in Eastern Cape waters there is potential competition between seals and the hake directed trawl fishery, horse mackerel trawl fishery, and the squid jig fishery.

Prey habitat

Of the 37 fish identified to species level, 29 (78.4%) were demersal, 3 (8.1%) were pelagic, 2 (5.4%) were bentho-pelagic, 2 (5.4%) were pelagic-midwater, and 1 (2.7%) was epipelagic-demersal. Of the 7 cephalopod identified, 43% were demersal and 57% were pelagic (Tables 9.5, 9.7, 9.9, 9.11). These observations suggest that on the Eastern Cape coast, seals forage extensively on the sea floor.

Interviews with experienced local fishermen

Interviews with experienced local fishermen (M. Brett, R. Colbold, A. Crawford, G. Edwards, A. Farquhar; B. Joubert, G. Lawrence, A. & C. Lilford) whom fish off the rocks at the Robberg Nature and Marine Reserve (Plettenberg Bay) indicate that 'on at least one occassion' seals have been observed feeding on: kob (*Argyrosomus hololepidotus*), galjoen (*Coracinus capensis*), red roman (*Chrysoblephus laticeps**), black musselcracker (*Cymatoceps nasutus**), springer/ladyfish (*Elops machnata**), southern mullet (*Liza richardsonii*), octopus sp., blue hottentot (*Pachymetopon aeneum**), spotted grunter (*Pomadasys commersonnii*), elf (*Pomatomus saltatrix*), lesser guitarfish (*Rhinobatos annulatus**), electric rays (*Torpedo sp.**) and blue-tail mullet (*Valamugil buchanani**). Seven of these records (marked with an astrict) add to the listing of seal prey species for the Eastern Cape coast.

Seal movement

Female 15990

SLTDR 15990 was deployed on March 19, 1993 and went offair on June 2, 1993, during which time a total of 34 valid locations were obtained (Figure 9.1 and 9.2).

Thirty (88%) recordings were within 10 km of Black Rocks. Mean distance from Black Rocks was 7.63 ± 2.38 km. The most southerly movement recorded was 34.075S, 25.68E, 60.12 km from Black Rocks. The most westerly movement was 34.075S, 25.68E, 60.12 km from Black Rocks. The most easterly movement was 33.863S, 36.321E, 5.95 km from Black Rocks.

Female 15989

SLTDR 15989 was deployed on September 15, 1994 and went off air on October 26, 1994, during which time a total of 26 locations were obtained (Figure 9.1 and 9.3).

Twenty (77%) recordings were within 10 km of Black Rocks. Mean distance from Black Rocks was 18.37 ± 7.64 km. The most southerly movement recorded was 34.478S, 26.466E, 73.44 km from Black Rocks. The most westerly movement was 33.814S, 26.2E, 6.52 km from Black Rocks. The most easterly movement was 34.308S, 28.088E, 176.23 km from Black Rocks.

Dive behaviour

Female 15990

A total of 277 'valid dives' were recorded for female 15990. Dive depth exceeded 160 m. Fifty one percent of dives were more than 60 m, of which 29% were 80–160 m. Deep dives, more than 160 m, represented only 4% of all dives.

The majority of dives (75%) were less than one minute in duration. Maximum dive duration was 2–3 minutes (Table 9.14, Fig. 9.4).

A bimodal distribution in the frequency of diving at different hours of the day was observed with most dives occurring near dawn (40% of all dives) and dusk (38% of all dives). The most frequently attained depth intervals were 60–80 m near dawn (34%); and 4–20 m (22%) and 80–160 m (26%) near dusk (Table 9.14, Fig. 9.5).

Female 15989

A total of 192 'valid dives' were recorded for female 15989. Dive depth exceeded 160 m. Sixty two percent of dives were more than 60 m, 48% of which were 80–160 m. Deep dives, more than 160 m, represented 12% of all dives.

The majority of dives (82%) were less than one minute in duration. Maximum dive duration was 3–5 minutes (Table 9.15, Fig. 9.4).

A bimodal distribution in the frequency of diving at different hours of the day was observed with most dives occurring near dawn (58% of all dives) and dusk (41% of all dives). The most frequently attained depth intervals were 60–80 m near dawn (45%); and surface (30%) and 80–160 m (36%) near dusk (Table 9.15, Fig. 9.5).

Table 9.14. ***Dive depth and duration summary data for female 15900 relative to time of day***

	Night	**Dawn**	**Day**	**Dusk**	**No. of dives (%)**
Depth					
surface	10.2	11.7	16.7	17.1	38 (13.72)
4–20	10.0	19.0	25.0	22.0	52 (18.77)
20–40	12.2	2.7	16.7	4.8	16 (5.78)
40–60	10.2	11.7	0.0	10.5	29 (10.47)
60–80	22.4	14.4	16.7	18.1	48 (17.33)
80–160	26.5	34.2	25.0	25.7	81 (29.24)
160^{+}	8.2	6.3	0.0	1.9	13 (4.69)
Total dives	**49**	**111**	**12**	**105**	**277**
Duration					
0–1	63.2	77.5	91.7	77.1	209 (75.45)
1–2	32.6	18.9	8.3	18.1	57 (20.58)
2–3	4.1	3.6	0.0	4.8	11 (3.97)
3–5	0.0	0.0	0.0	0.0	0
5–7	0.0	0.0	0.0	0.0	0
7^{+}	0.0	0.0	0.0	0.0	0
Total (minutes)	**40.53**	**67.91**	**4.15**	**71.51**	**277**

Based on local time (= GMT + 2 hrs)

Night (2100–0259 hrs); dawn (0300–0859 hrs); day (0900–1459 hrs); and dusk (1500–2059 hrs).

Table 9.15. ***Dive depth and duration summary data for female 15989 relative to time of day***

	Night	**Dawn**	**Day**	**Dusk**	**No. of dives (%)**
Depth					
surface	0	6.3	0	29.5	30 (15.63)
4–20	0	9.0	50	9.0	18 (9.38)
20–40	0	9.9	50	6.4	17 (8.85)
40–60	0	5.4	0	2.6	8 (4.17)
60–80	0	9.0	0	10.6	18 (9.38)
80–160	0	45.0	0	35.9	78 (40.63)
160^{+}	100	15.3	0	6.4	23 (11.98)
Total dives	**1**	**111**	**2**	**78**	**192**
Duration					
0–1	100	79.3	100	85.9	158 (82.30)
1–2	0	20.7	0	11.6	32 (16.70)
2–3	0	0	0	1.3	1 (0.52)
3–5	0	0	0	1.3	1 (0.52)
5–7	0	0	0	0	0
7^{+}	0	0	0	0	0
Total (minutes)	**0.35**	**75.03**	**1.83**	**39.23**	**192**

Based on local time (= GMT + 2 hrs)

Night (2100–0259 hrs); dawn (0300–0859 hrs); day (0900–1459 hrs); anddusk (1500–2059 hrs).

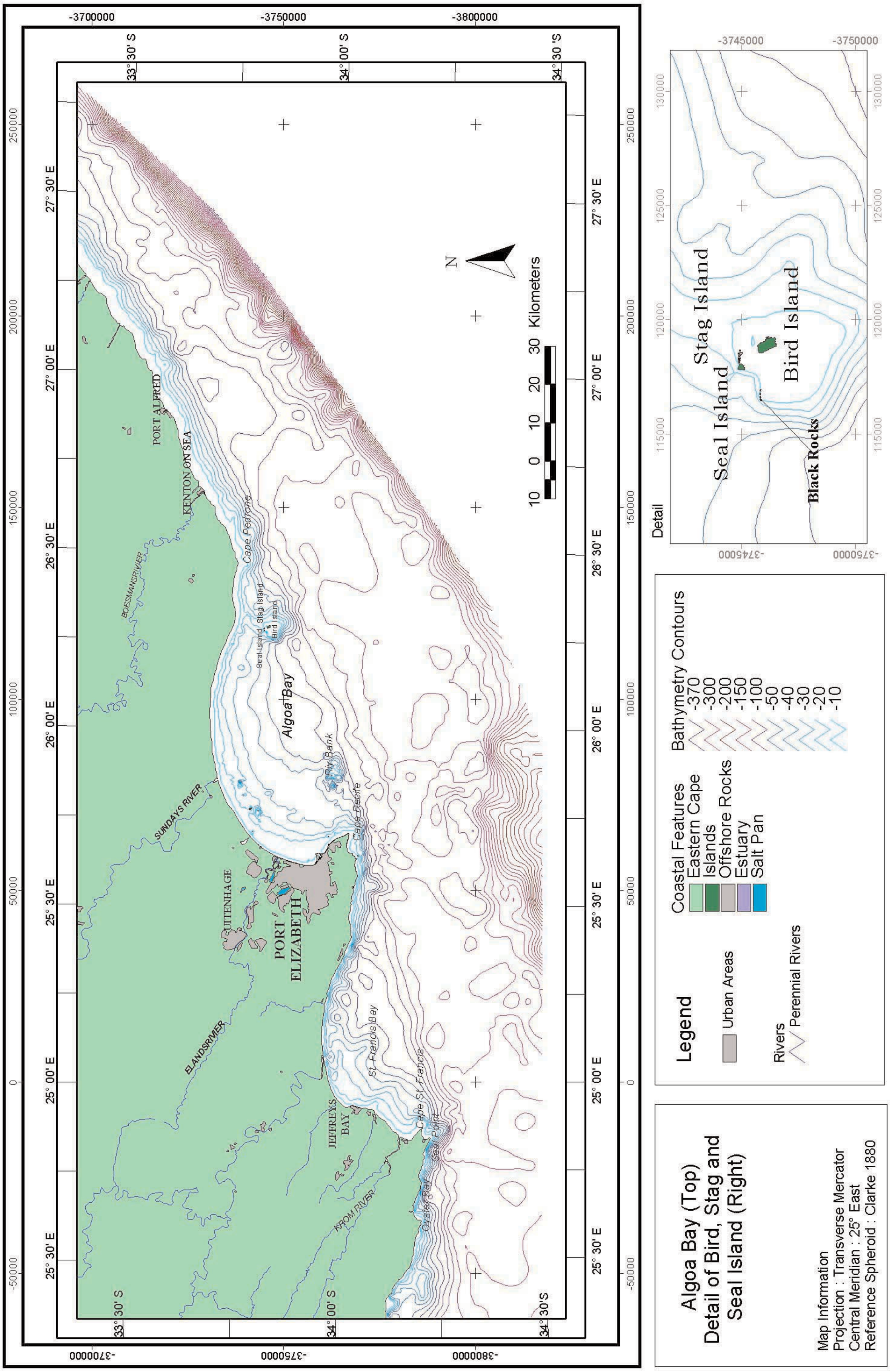


Fig. 9.1 Bathymetry of Black Rocks study area.

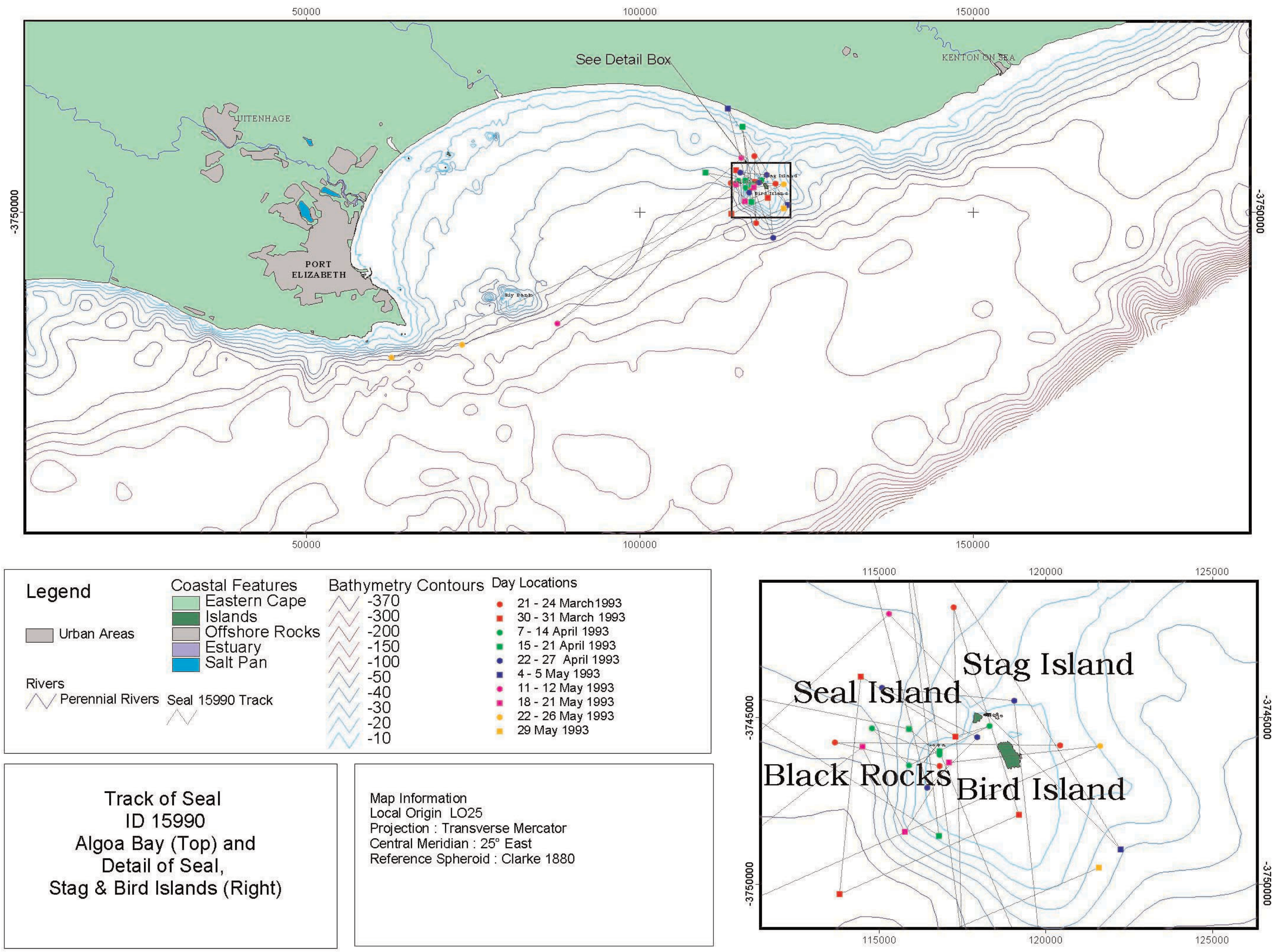


Fig. 9.2 Black Rocks study area showing SLTDR locations of an adult female Cape fur seal.
SLTDR 15990 was deployed at Black Rocks (Algoa Bay) on September 15, 1993, and went off the air on October 26, 1993.

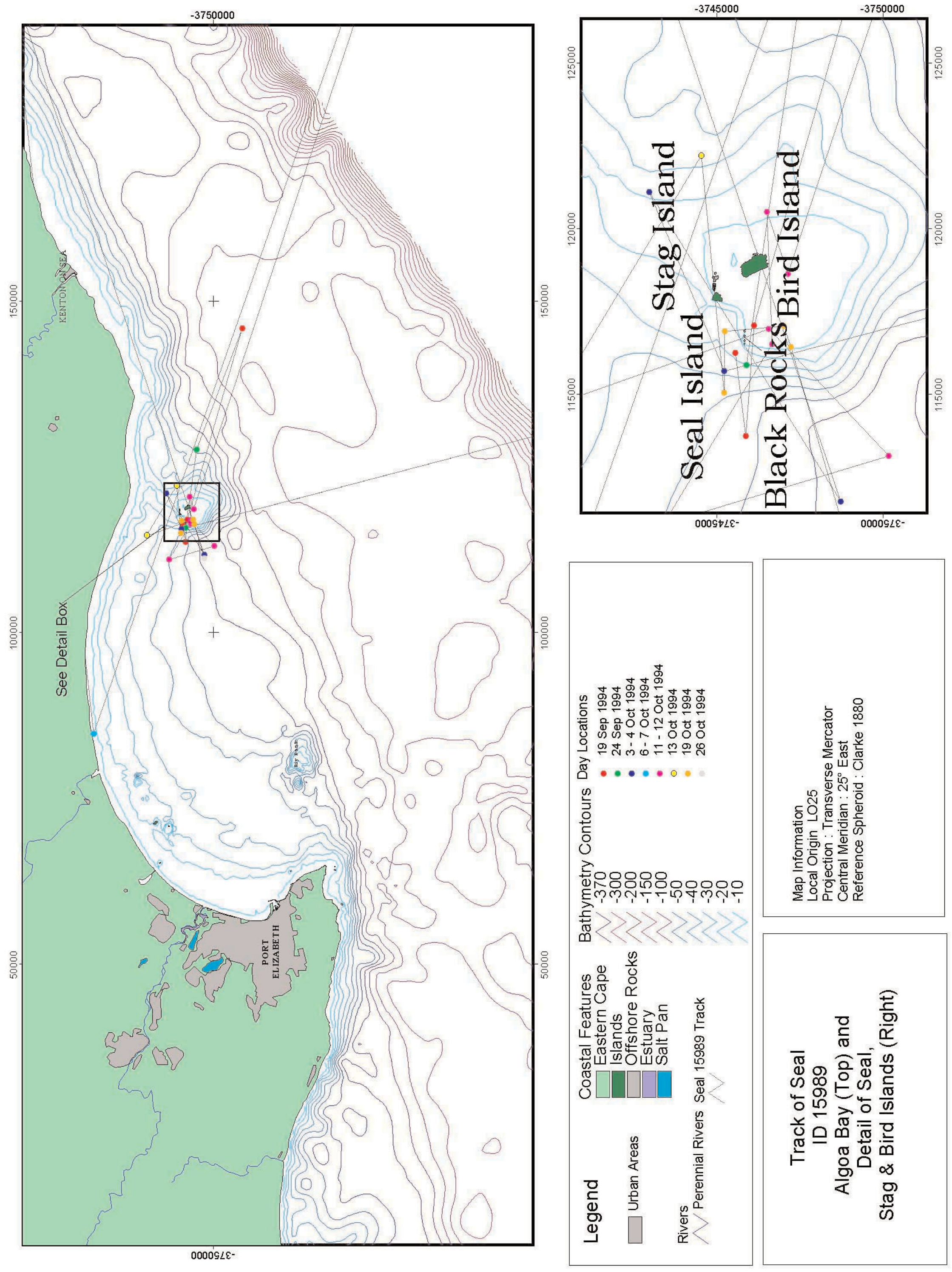
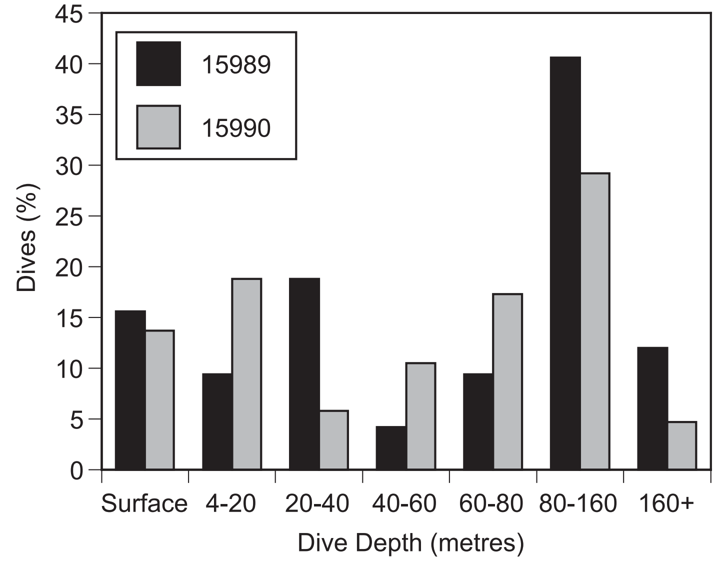


Fig. 9.3 Black Rocks study area showing SLTDR locations of an adult female Cape fur seal.
SLTDR 15989 was deployed at Black Rocks (Algoa Bay) on September 15, 1994, and went off the air on October 26, 1994.



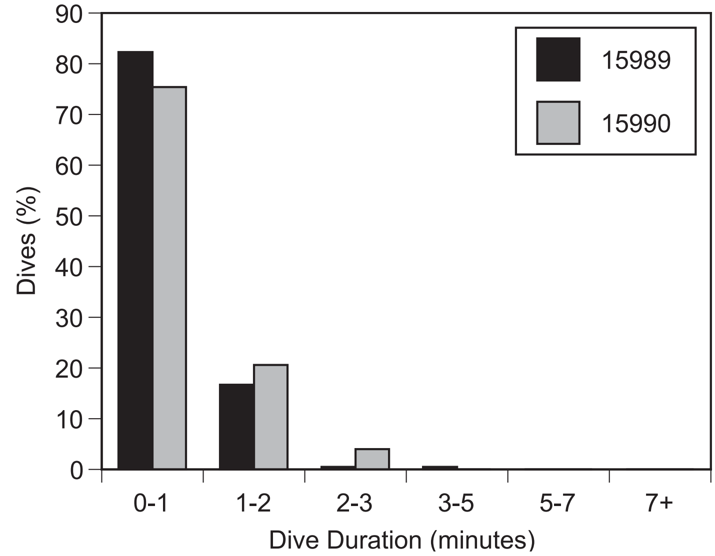


Fig. 9.4 Dive depth frequency and dive duration frequency.
Data is for two adult female Cape fur seals (SLTDR 15900 and SLTDR 15989) tagged at Black Rocks, Algoa Bay.

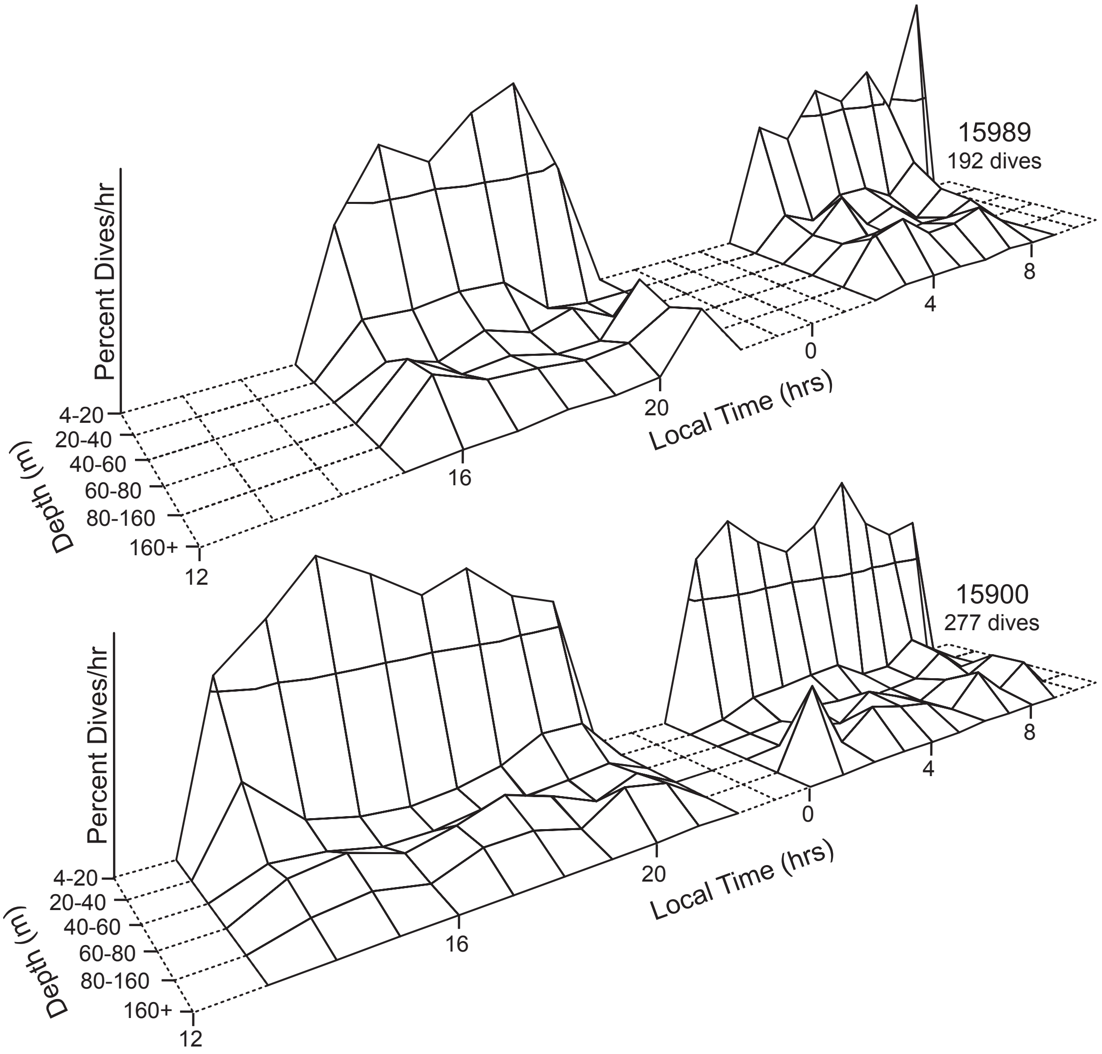


Fig. 9.5 Three-dimensional frequency analysis for depth of dive, time of day, and number of dives.
Data is for two adult female Cape fur seals (SLTDR 15900 and SLTDR 15989) tagged at Black Rocks, Algoa Bay.

DISCUSSION

Potential bias in seal dietary studies

In the present study, killing of animals was not desired, therefore non-lethal methods were used to acquire dietary samples, i.e., the collection of: (i) faecal samples (and regurgitates if present); (ii) stomach contents from stranded animals; and (iii) stomach contents from animals drowned incidentally in trawl nets. As with all methods of acquiring seal dietary samples, known biases are associated with these methods which prevent an accurate quantitative assessment of the data. Furthermore, there is no single method of presenting results which is free from bias (Croxall, 1993).

The use of fish otoliths to determine composition of the diet is potentially bias because: (i) some otoliths may be completely digested in the gastrointestinal tract (especially smaller fragile otoliths), therefore they may be underestimated in the stomach and faeces; (ii) some otoliths may be partially digested in the gastrointestinal tract, therefore they may not always represent the size of fish ingested; and (iii) large fish may be underestimated if the heads (otoliths) are not eaten (Boulva & McLaren, 1979; Brown & Mate, 1983; da Silva & Neilson, 1985; Murie & Lavigne, 1985; Prime & Hammond, 1987; Härkönen, 1986; Dellinger & Trillmich, 1988; Harvey, 1989; Gales & Cheal, 1992).

Use of cephalopod beaks to determine composition of the diet is potentially bias because: (i) the irregular shape of the beaks makes then prone to retention in the stomach folds, therefore they may be overestimated in the stomach and underestimated in the faeces; (ii) beaks are often regurgitated, therefore they may be underestimated in the stomach and faeces; and (iii) smaller beaks may pass through the pylorus of the stomach more easily than larger beaks, therefore, larger cephalopod prey may be underestimated in faeces (Miller, 1978; Pitcher, 1980; Bigg & Fawcett, 1985; Richardson & Gales, 1987; Gales & Cheal, 1992).

The use of stomach contents from stranded animals is potentially bias because: (i) stranded animals may have died of injury or illness, therefore stranded animals may be less selective about prey species than healthy ones; and (ii) due to the extended period of fasting, cephalopod remains may be overestimated and fish remains may be underestimated (Selzer *et al.,* 1986; Gales & Cheal, 1992).

Therefore, to minimise potential biases in the present study, only otoliths with little or no obvious erosion were measured; regurgitates were collected if present; and composition of the diet was presented using several methods, i.e., by number, frequency of occurrence, and mass.

Composition of the diet

On the Eastern Cape coast, Cape fur seals are opportunistic feeders, and take predominantly benthic prey. Prey species recovered from dietary samples included 37 species of fish, 7 species of cephalopods, a small number of crustacea (mostly decapoda), and other miscellaneous items, i.e., African penguin feathers (*Spheniscus demersus*), dogfish shark egg cases (*Squalus* sp.), unidentified molluscs, stones and seaweed.

The most important prey species (by percent mass) in the stomach contents of stranded seals were *L. vulgaris reynaudii*, *T. trachurus capensis*, *P. bellottii natalensis*, *E. whiteheadi* and *C. zanzibarensis/ capensis*. However, the predominance of *L. vulgaris reynaudii* is likely to be overestimated due to the extended period of fasting prior to death.

The most important prey species (by percent mass) in the stomach contents of seals incidentally caught in commercial trawl nets were *L. caudatus*, *M. capensis/paradoxus*, *T. trachurus capensis* and *O. magnificus*. *L. caudatus* is often caught in trawl nets as by-catch. Discarded by-catch is frequently eaten by adult male Cape fur seals (Stewardson, pers. obs).

The most important prey species (by number and frequency of occurrence[1]) in faecal samples and regurgitates at Black Rocks were *L. vulgaris reynaudii T. trachurus capensis* and *S. ocellatus*; whereas the most important prey species (by number and frequency of occurrence[1]) in faecal samples at Rondeklippe were *C. zanzibarensis/capensis*, *A. pectoralis*, *S. ocellatus* and *T. trachurus capensis*. Preliminary studies examining otoliths in faecal samples from four captive Cape fur seals suggest that: (i) fish otoliths pass through the seal's digestive tract within 24–48 hrs of ingestion; (ii) the recovery rate of otoliths in the faeces is > 58%; (iii) the mean length of reduction of otoliths recovered from faeces is *c.* 23%; and (iv) *c.* 25% of left and right otoliths recovered in the faeces are uneroded (Millar, Wickens & Lowry, pers. comm.). Therefore, in the present study, it is likely that: (i) some of the prey items were not consumed over a one day period; (ii) larger, more robust otoliths were likely to be overestimated and smaller, fragile otoliths were likely to be underestimated; and (iii) the estimated original sizes derived from the regression equations will be underestimated. Furthermore, the predominance of *L. vulgaris reynaudii* at Black Rocks is likely to be overestimated because regurgitates may represent several meals over several days.

David (1987) examined stomach contents of *c.* 1 000 Cape fur seals shot at sea between Namibia and the south coast of South Africa, from 1974 to 1985. He reported that on the Namibian coast, teleost fish contributed 90.6% to the diet, cephalopods 8.2% and crustaceans 1.2%; and the most important species were pelagic goby (*Sufflogobius bibarbatus*) and *T. trachurus capensis* (*n* = 302 stomachs). On the west coast of South Africa, teleost fish contributed 64.4% to the diet, cephalopods 18.4%, crustaceans 9.3%, rock lobster 6.8% and elasmobranchs 1.0%; and the most important species were *E. capensis* and *M. capensis/pardadoxus* (*n* = 279 stomachs). On the south coast of South Africa, teleost fish contributed 67.7% to the diet, cephalopods 29.7%, crustaceans 1.2% and elasmobranchs 1.2%; and the most important prey species were *E. capensis*, *T. trachurus capensis*, *M. capensis/pardadoxus* and *S. ocellatus* (*n* = 115 stomachs). Differences in collection area and collection methods prevented direct comparison with the present study. However, four prey species (*T. trachurus capensis*, *M. capensis/pardadoxus* and *S. ocellatus*) which were found to be important on the south coast (David, 1987), were also identified as important prey species in Eastern Cape waters (present study). Furthermore, teleost fish were also found to be the most important prey group overall, i.e., teleost fish (41–94%), cephalopods (4–57%), crustaceans (0.9–7%), and miscellaneous items (0.2–5%) (present study).

Castley *et al.,* (1991) reported that the most important prey species (by percent total mass) isolated from the stomachs of 36 stranded Cape fur seals collected between Knysna and East London from 1976 to 1990 were *L. vulgaris reynaudii* (34.5%), *M. capensis* (24.1%), *T. trachurus capensis* (12.6%) and *C. zanzibarensis* (7.7%). In the present study, the most important prey species (by percent total mass) were *L. vulgaris reynaudii* (54%), *T. trachurus capensis* (28%), *P. bellottii natalensis* (8%), *E. whiteheadi* (4%) and *C. zanzibarensis/capensis* (3%). Castley *et al.,* (1991) identified 14 fish species and 7 cephalopod species in the stomach contents of stranded seals. All species reported by Castley *et al.,* (1991) were identified in the present study apart from *Cheimerius nufar*, *Chelidonichthys capensis*, *Argonauta nodosa*, *Ocythoe tuberculata* and *Onychoteuthis banksi*.

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[1] Percent number and percent frequency of a given species are both of a high magnitude.

Regional variation in diet based on faecal analysis at the two seal colonies

The most important prey species (by number and frequency of occurrence[1]) in faecal samples and regurgitations at Black Rocks were *L. vulgaris reynaudii T. trachurus capensis* and *S. ocellatus*; whereas the most important prey species (by number and frequency of occurrence[1]) in faecal samples at Rondeklippe were *C. zanzibarensis/capensis*, *A. pectoralis*, *S. ocellatus* and *T. trachurus capensis*.

These differences are likely to reflect temporal and geographical differences in the abundance of certain prey species. For example, the main sole (*A. pectoralis* and *Cynoglossus* sp.) trawling grounds lie between Struis Bay and Plettenberg Bay, near the Rondeklippe seal colony, where there is considerable 'muddy bottom' habitat suitable for sole. In contrast, there are only isolated patches of 'muddy bottom' habitat between Cape St Francis and East London, near the Black Rocks seal colony (Payne & Badenhorst, 1995).

Differences in the age and/or sex of animals at the two sites; differences in the foraging range of seals with respect to water depth, temperature and bottom topography; and differences in collection methods, would also contribute to observed differences.

Potential competition between seals and fisheries

Eastern Cape trawl fishery

The most important trawl species in Eastern Cape waters (*Merluccius capensis*, *Merluccius paradoxus*, *Trachurus trachurus capensis* and *Austroglossus pectoralis*) are also important prey species of Cape fur seals (present study).

The modal size of *M. capensis* taken by Cape fur seals in this study was 287.73 mm, which was within the size range of local commercial catches (30–980 mm) (Table 9.13). The modal size of *M. paradoxus* was 309.59 mm, which was also within the size range of local commercial catches, e.g., 60–850 mm (Table 9.13). *M. capensis* inhabits the shelf and slope to 400 m, whereas *M. paradoxus* is generally found in deeper water (200–1 000 m) (Smith & Heemstra, 1986). Most hake migrate upwards at dusk and return to the sea bed at dawn. Satellite telemetry suggests that Cape fur seals feed mainly around dawn and dusk (present study). Therefore, it is likely that seals feed on hake when hake are near the water surface at night. Adult male seals also take hake during the day when they follow trawlers, e.g., feed on discarded offal and small hake which float free from the net (Stewardson, pers. obs.).

Modal size of *T. trachurus capensis* taken by Cape fur seals was 184.82 mm, which was within the size range of local commercial catches, e.g., 60–560 mm (Table 9.13). Smaller horse mackerel feed near the water surface, whereas older horse mackerel feed predominantly in midwater. At night, older horse mackerel form dense concentrations away from the sea bed. During the day these concentrations break down and individuals settle near the sea bed (Crawford, 1995). It is likely that seals feed on older horse mackerel when horse mackerel are away from the sea bed at night. Adult male seals also take horse mackerel during the day when they scavenge from trawlers (Stewardson, pers. obs.).

Commercially important *A. pectoralis* also contributed significantly to the diet of seals in this area. Modal size taken by Cape fur seals in this study was 232.70 mm ($n = 281$), which is within the range of local commercial catches, e.g., range 30–590 mm. However, the inshore sole directed trawl fishery operates south/south-west of the study area and is therefore excluded for further discussion.

Many species taken by Cape fur seals occur as trawl by-catch, including kingklip (*Genypterus capensis*), John dory (*Zeus faber*), monk fish (*Lophius* sp.), ribbon fish (*Lepidopus caudatus*), jacopever (*Helicolenus dactylopterus*), reds (e.g., capenter, *Argyrozona argyrozona*; panga *Pterogymnus laniarius*), chub mackerel, *Scomber japonicus* and chokker squid. Adult males are frequently observed following trawl vessels, feeding on offal and by-catch (Stewardson, pers. obs).

Squid jig fishery

Since the early 1980s, there has been a substantial chokker squid jigging fishery in Eastern Cape waters, between Plettenberg Bay and Port Elizabeth. The modal mantle length of chokker squid jig catches in these waters is *c.* 290 mm for males and *c.* 180 mm for females (Augustyn & Smale, 1995). Modal size taken by Cape fur seals is 229.96 mm (present study), which is within the range of local commercial catches (Table 9.13).

Chokker squid is a pelagic species. It undertakes daily vertical migrations, and is found to 300 m depth. It is likely that seals feed on chokker squid when the squid move towards the surface at night. In summer, chokker squid moves inshore to spawn, laying their eggs in shallow bays (15–40 m) between Plettenberg Bay and Port Elizabeth. It is likely that at this time of the year, chokker is consumed in larger quantities, and is taken at day and night.

Teleost line fishery

The main line fish species in Eastern Cape waters, which are also taken by Cape fur seals, include hake (*Merluccius* sp.), silver fish *(Argyrozona argyrozona*), panga (*Pterogymnus laniarius*), kob *(Argyrosomus hololepidotus*), dageraad (*Chrysoblephus cristiceps*), mackerel (*Scomber japonicus*) and elf (*Pomatomus*

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[1] Percent number and percent frequency of a given species are both of a high magnitude.

saltatrix). Currently, size frequency distribution for the Eastern Cape line fisheries is not available (Chris Wilke, pers. comm.).

Annual consumption by seals

The total annual consumption of prey for Cape fur seals in Eastern Cape waters can be obtained by multiplying the number of foraging animals, by the estimated average daily ration, by 365 days.

At least some seals from Seal Island (Mossel Bay) feed in Eastern Cape waters. Therefore, inorder to estimate annual consuption in this region, the total estimated population for Black Rocks and Mossel Bay was combined. Pup numbers at Black Rocks were 463 in 1992 and 296 in 1996 (Marine & Coastal Management, unpubl. data). Pup numbers at Mossel Bay were 754 in 1992 and 989 in 1996 (Marine & Coastal Management, unpubl. data). Therefore, the combined estimated size of the population in the general area is 6 085 in 1992 and 6 425 in 1996 (i.e., the estimated total pup number was multiplied by 5).

The estimated average daily ration for Cape fur seals is *c.* 3.2 kg (Meÿer *et al.,* 1992). Hence, estimated total annual consumption was:

$$6\,085 \times 3.2 \times 365 = 7\,107 \text{ tons in 1992}$$

$$6\,425 \times 3.2 \times 365 = 7\,504 \text{ tons in 1996}$$

This will be a maximum estimate of total consumption because it includes animals < 1 year, which do not forage.

Diving behaviour and movement patterns

A bimodal distribution in the frequency of diving at different hours of the day was observed, with most dives occurring near dawn and dusk (present study). A similar dive pattern has also been reported in two female Cape fur seals at Kleinsee on the west coast of South Africa (Kooyman & Gentry, 1986), and in several female northern fur seals at St. George Island (Gentry *et al.,* 1986). Activity near dawn and dusk may be associated with changes in the accessibility of some important prey species. For example, *L. vulgaris reynaudii*, *M. capensis* and *T. trachurus capensis* move away from the sea bed at night. Observed activity patterns may also be associated with an increase in prey vulnerability at this time of the day. Some fish are more susceptible to predation at dawn and dusk when available light wavelengths in the water column rapidly shift out of their range of peak spectral sensitivity (Gentry *et al.,* 1986).

In the present study, the most frequently attained depth range was 80–160 m. In comparison, Kooyman & Gentry (1986) reported that the most frequently attained depth for two female Cape fur seals was ≤ 50 m, but dives to 100 m were common; and Gentry *et al.,* (1986) reported that the most frequently attained depths for seven northern fur seals were 50–60 m and 175 m.

In the present study, the majority of dives (75–82%) were less than one minute in duration, with a maximum dive duration of 3–5 minutes. In comparison, Kooyman & Gentry (1986) reported that the maximum dive duration for two female Cape fur seals was 2.1 minutes, with a maximum dive duration of 7.5 minutes; and Gentry *et al.,* (1986) reported that the maximum dive duration for seven female northern fur seals was 2.6 minutes, with a maximum dive duration of 5–7 minutes.

Maximum dive depth for both females exceeded 160 m (present study). In comparison, Kooyman & Gentry (1986) reported that the maximum dive depth for two female Cape fur seals was 204 m; and Gentry *et al.,* (1986) reported that the maximum dive depth for seven female northern fur seals was 207 m. In the present study, deep dives, more than 160 m, represented 4% of dives for female 15 990 and 12% of dives for female 15 989 (present study). This indicates that a small proportion of dives were made at or near the continental shelf break (200 isobath contour).

Positional data indicated that females with pups tend to forage close to the colony (i.e., usually within 10–18 km). However, they can travel long distances in search of food, e.g, 60–70 km south of the colony.

CONCLUSION

Known biases associated with the collection of seal dietary samples prevented an accurate quantitative assessment of the data. However, results indicate that Cape fur seals are opportunistic feeders and take predominantly benthic prey, including 37 species of teleost fish, 7 species of cephalopod, a small number of crustacea (mostly decapoda), and other miscellaneous items. *T. trachurus capensis*, *M. capensis/paradoxus*, and *S. ocellatus* were the most important prey species overall. Differences in the composition of the diet at Black Rocks and Rondeklippe are likely to reflect temporal and geographical differences. The model size of *M. capensis*, *M. paradoxus*, *T. trachurus capensis*, *A. pectoralis* and *L. vulgaris reynaudii* consumed by Cape fur seals fell within the range of local commercial catches, indicating potential competition between seals and the fisheries in this region. A bimodal distribution in the frequency of diving at different hours of the day was observed, with most dives occurring near dawn (± 3 hours) and dusk (± 3 hours) (n = 2 females). This activity may be associated with changes in the accessibility of some important prey species (e.g., *L. vulgaris reynaudii*, *M. capensis* and *T. trachurus capensis*) and/or changes in prey vulnerability.

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PART 6

CONSERVATION BIOLOGY

PLATES 6–13

Plate 6 Black Rocks, Algoa Bay (South Africa)

6.1

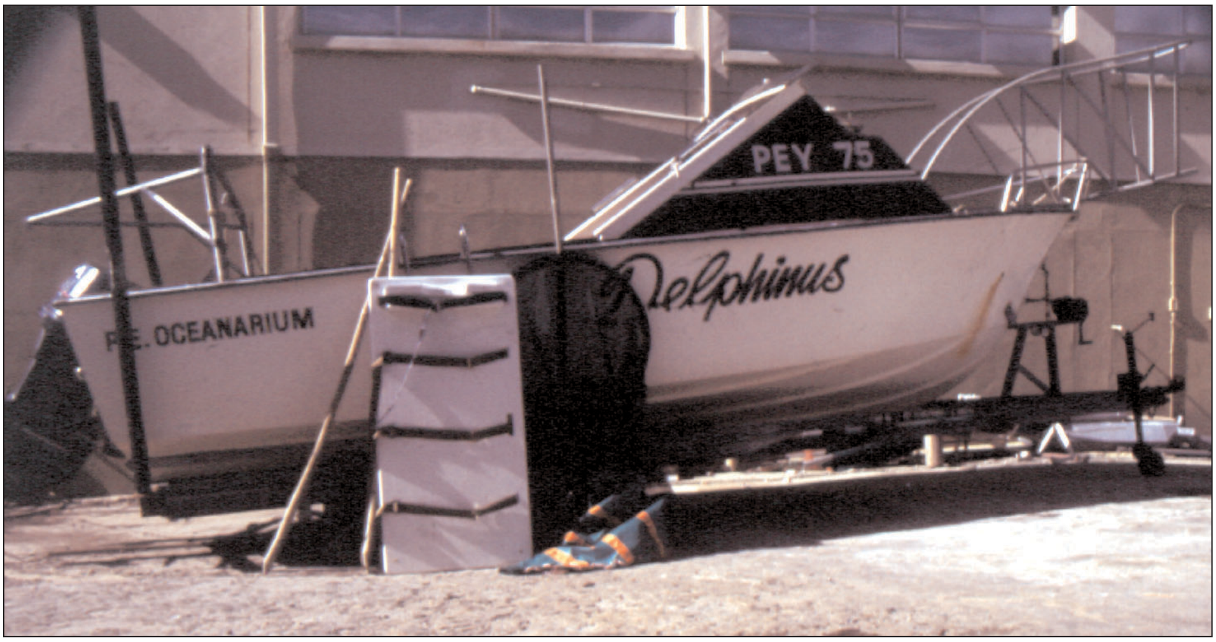
6.1 Black Rocks in the foreground, ~ 5 nm from land. Stag and Seal Islands to the right. Alexandra State Forest in the background (photo: E. Pike).

Plate 7 Field trips to Black Rocks

7.1

7.2

7.3



7.4

7.1–7. 3 The Cape Nature Conservation rubber duck was used to commute to Black Rocks. It was launched from the nearest suitable beach, 7–15 nm from Black Rocks, e.g., Alexandra State Forest beach; Cannon Rocks (photos 7.1 & 7.2: C. Stewardson; photo 7.3: C. Urquhart).

7.4 The Port Elizabeth Museum ski boat (*Delphinus*) was occasionally used to commute between Port Elizabeth and Black Rocks, a 68 nm round trip (photo: C. Stewardson).

Plate 8(a) Pup mortality attributed to storms

8.1

8.2

8.3

8.4

8.1 Waves breaking over Black Rocks (photos: C. Stewardson).

8.2–8.4 Pups are introduced to the water when only a few hours old; however they acquire swimming abilities slowly, gaining proficiency only after some months of 'training' in the rock pools. If storms occur during the pupping season (Nov–Dec), many pups may be washed from the rocks (photos: C. Stewardson).

Plate 8(b) Pup mortality attributed to storms

8.5

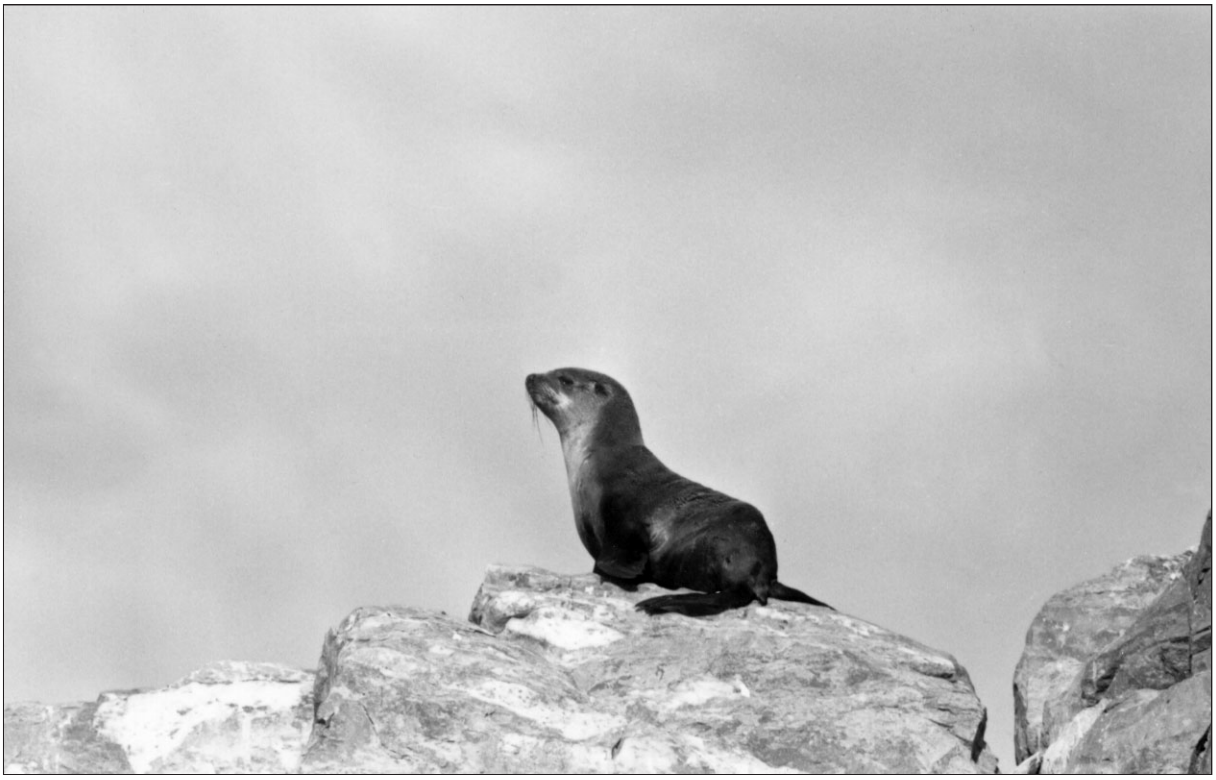
8.6

8.7

8.8

8.5–8.8 For the purpose of this study, a weather station was established on Bird Island < 1 nm east of Black Rocks seal colony. Wind speeds and directions were measured using a pressure plate anemometer (photos 8.5, 8.6 & 8.8: C. Stewardson; photo 8.7: H. Watts).

Plate 9 Fur seal industry



9.1

9.2

9.1 & 9.2 Before commercial exploitation by Europeans began in 1610, Cape fur seals inhabited six islands in Algoa Bay (Seal, Stag, Black Rocks, St. Croix, Jahleel and Brenton). By the early 1900s, all Eastern Cape colonies were extirpated, with the exception of Black Rocks. Here, a lone Cape fur seal hauls-out on St. Croix Island. Available evidence suggests that seals were extripated from the St. Croix Islands in the late 1850s (photos: G. Ross).

Plate 10(a) Fisheries

10.1

10.2

10.3

10.4

10.1 & 10.2 Fishing vessels at Port Elizabeth harbour (photos: C. Stewardson).
10.3 & 10.4 Stern trawlers operating on commercial fishing grounds off the Eastern Cape coast (photos: C. Stewardson).

Plate 10(b) Fisheries

10.5

10.6

10.7

10.8

10.5–10.8 Stern trawlers operating on commercial fishing grounds off the Eastern Cape coast (photos: C. Stewardson).

Plate 10(c) Fisheries

10.9

10.10

10.9 & 10.10 The fishermen (photos: C. Stewardson).

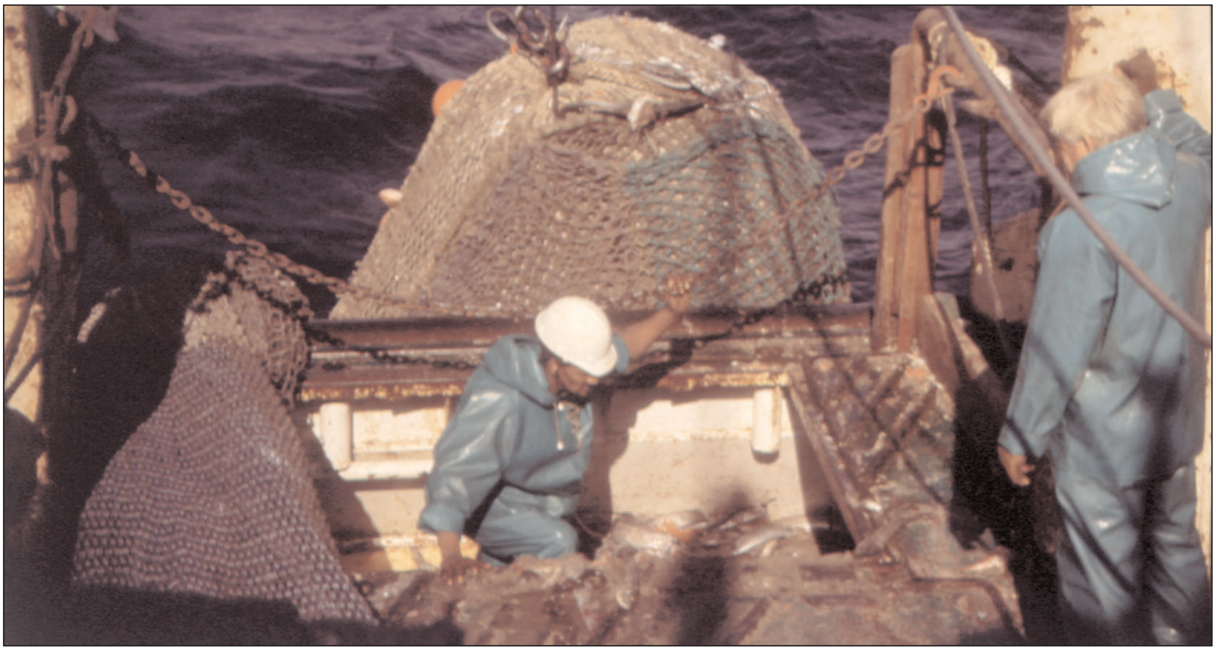
Plate 10(d) Fisheries

10.11

10.12

10.11 & 10.12 The fishermen (photos: C. Stewardson).

Plate 10(e) Fisheries



10.13

10.14

10.15

10.16

10.13 & 10.14 Stern trawlers (photos: C. Stewardson).

10.15 & 10.16 Side trawlers (photos: C. Stewardson).

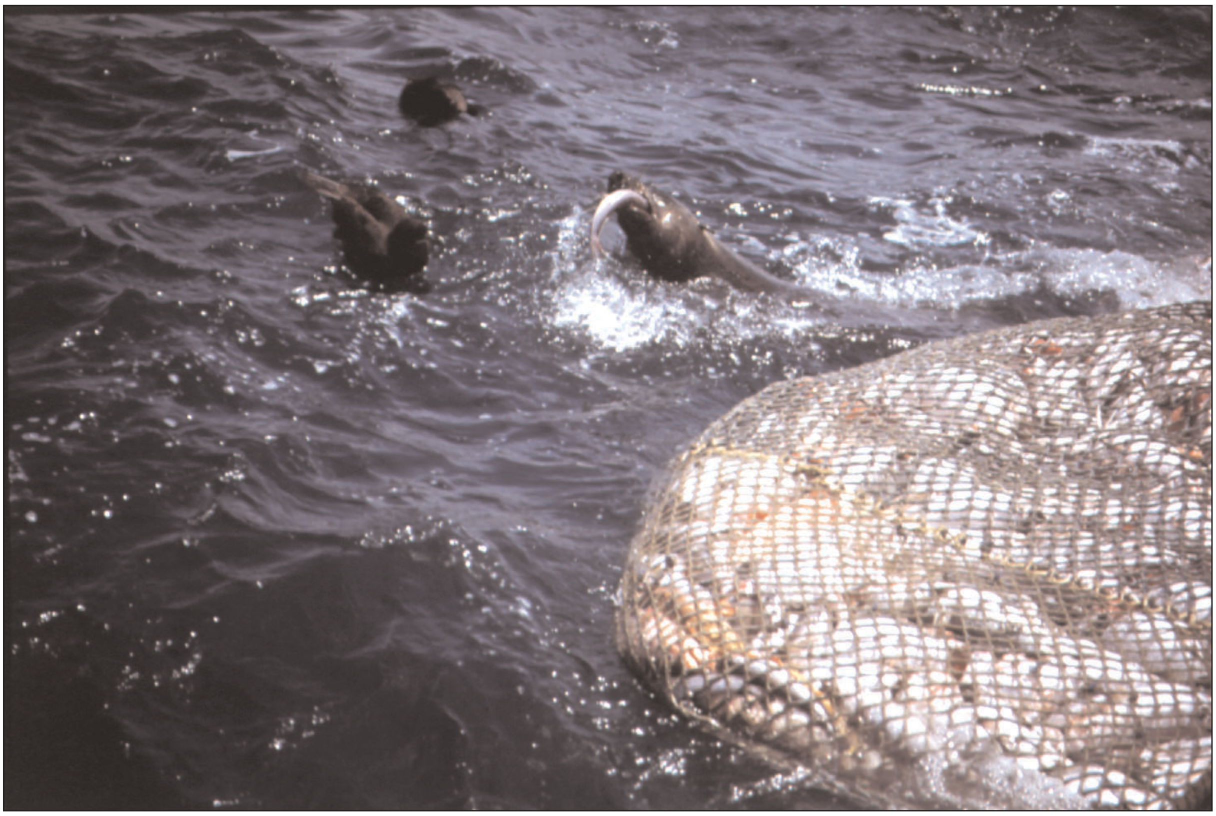
Plate 11(a) Seal-fisheries interactions

11.1

11.2

11.1 & 11.2 Seals taking fish from the net of a side trawler. The catch is mainly hake and kingklip (photos: C. Stewardson).

Plate 11(b) Seal-fisheries interactions



11.3

11.4

11.3 & 11.4 Seals taking fish from the net of a side trawler. The catch is mainly hake and kingklip (photos: C. Stewardson).

Plate 11(c) Seal-fisheries interactions

11.5

11.6

11.7

11.8

11.5 Fish which protrude from trawl nets, while the net is being brought to the surface, are easily taken by seals. Here we have the tail of a kingklip, and small fish protruding from the net (photo: C. Stewardson).

11.6 Seals feed on ribbon fish and hake heads discarded from the trawlers, i.e., by-catch and offal (photo: C. Stewardson).

11.7 Hakes damaged by seals feeding from trawl nets (photo: C. Stewardson).

11.8 By-catch is usually thrown overboard (photo: C. Stewardson).

Plate 11(d) Seal-fisheries interactions

11.9

11.10

11.9 & 11.10 Seals are incidentally caught in nets during commercial fishing operations (photos: C. Stewardson).

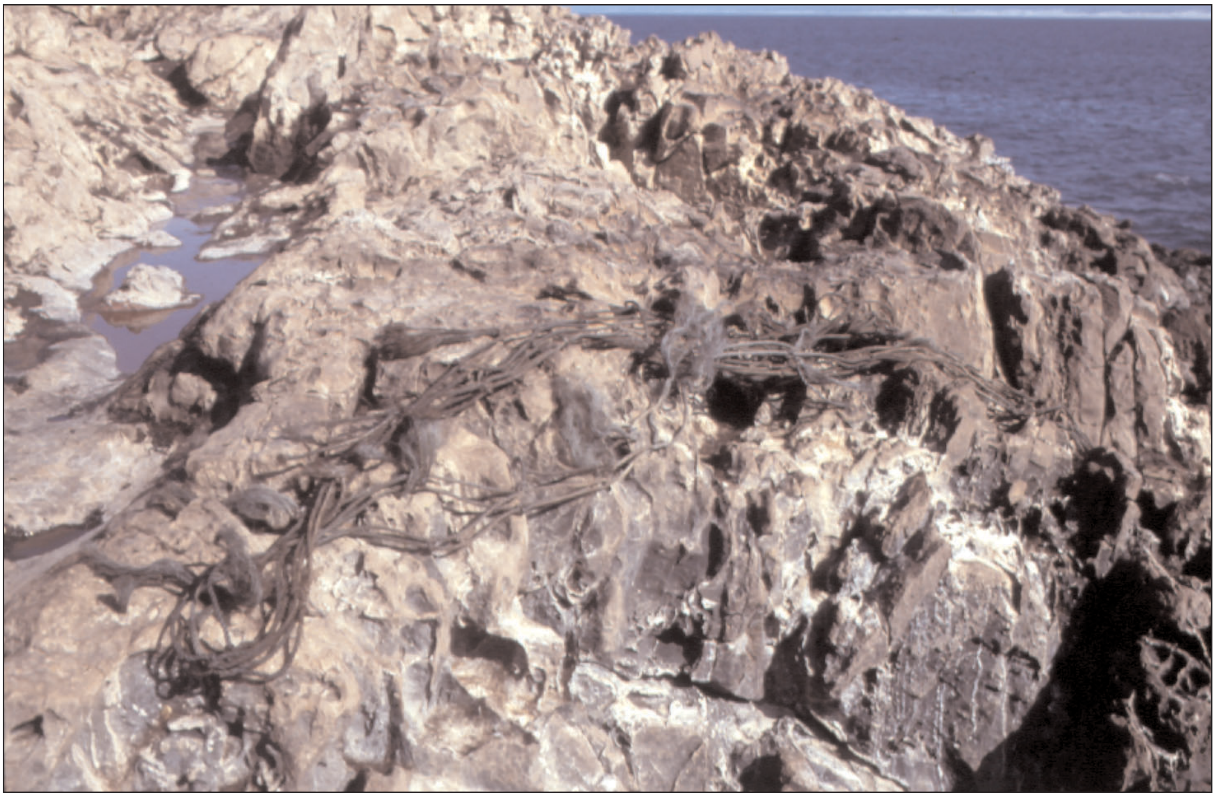
Plate 11(e) Seal-fisheries interactions

11.11

11.12

11.11 & 11.12 Shooting of seals by fisherman is a contributing factor to the overall mortality of Eastern Cape seals (photos: C. Urquhart).

Plate 12(a) Entanglement



12.1

12.2

12.1 Piece of discarded trawl net washed up on Black Rocks (photo: C. Urquhart).
12.2 Adult seal entangled in trawl net (photo: C. Stewardson).

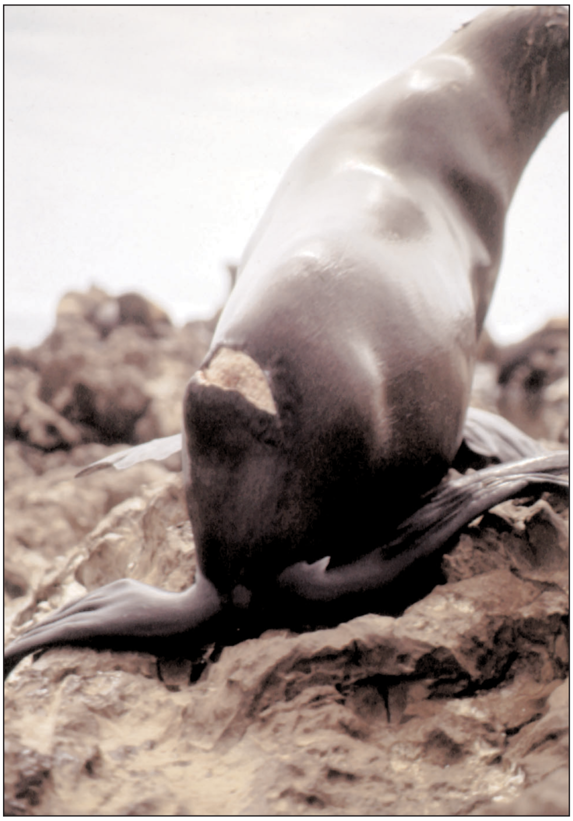
Plate 12(b) Entanglement

12.3

12.4

12.3 & 12.4 Seals at Black Rocks entangled in rope–'necklace of death' (photos: C. Urquhart).

Plate 13 Shark predation



13.1

13.2

13.3

13.4

13.1–13.4 Seals at Black Rocks with shark inflicted injuries (photos 13.1, 13.3 & 13.4: C. Stewardson; photo 13.2: C. Urquhart).

CHAPTER 10(a)

The Impact of the fur seal industry on the distribution and abundance of Cape fur seals *Arctocephalus pusillus pusillus* on the Eastern Cape coast of South Africa

C. L. Stewardson

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ABSTRACT

The present paper provides a review of the former distribution and abundance of Cape fur seals, *Arctocephalus pusillus pusillus*, off the Eastern Cape coast of South Africa based on available historical records. It identifies the distribution of Eastern Cape seals before commercial sealing began; documents sealing activities off the Eastern Cape coast during the 19th and 20th centuries, and discusses current population trends in relation to past exploitation regimes. The importance of the Eastern Cape population is discussed in relation to the total population. Cape fur seals were valued primarily for their fine quality furs. Other products included oil from the blubber; leather from skins of old seals; and vitamin A from the liver. Exploitation by Europeans began near the Cape of Good Hope in 1610. By the end of the 19th century more than 20 colonies had been extirpated. On the Eastern Cape coast, Cape fur seals inhabited six islands in Algoa Bay (Stag, Seal, Black Rocks, St. Croix, Jahleel and Brenton) and two sites in Plettenberg Bay (Seal Point on the Robberg Peninsula and Beacon Island). Soon after British settlement of Algoa Bay in 1820, the St. Croix and Bird Islands were leased to individuals by the governor of the Cape Colony (Lord Charles Sommerset) at an annual rental, for fishing and sealing purposes. More than 18 000 seals were killed by commercial sealers in Algoa Bay between 1822 and 1825; > 2 935 between 1831 and 1850; c. 3 516 between 1851 and 1876; > 1763 in 1907 and 1908; and > 500 between 1943 and 1949. Harvest figures for Plettenberg Bay are unknown. Available evidence suggests that seals had been extirpated from St. Croix, Jahleel and Brenton Islands in the late 1850s; Seal Point between 1857 and 1890; Stag Island in the mid/late 1800s; Seal Island in the early 1900s; and Beacon Island in the late 1800s/early 1900s. Black Rocks was the only colony on the Eastern Cape coast to survive commercial sealing operations. Access to Black Rocks is difficult and for that reason sealing activities were irregular. Sealing operations on Black Rocks were terminated in 1949. At present, Black Rocks supports *c.* 700 seals. In the last 12 years (1986–1997) the population has decreased by 82%. By destroying seal herds through commercial harvesting, and confining the population to Black Rocks, the population is unable to build up its numbers sufficiently to stimulate colonisation on neighbouring islands. Limited space for breeding seals on Black Rocks, and the influence of storms (gale force winds and high swells) restricts the number of pups that can be reared successfully. It is unlikely that the Black Rocks population can increase quickly enough to flow onto Seal and Stag Island, without being depleted by storms. The effect of man on the Seal, Stag and Black Rocks population is therefore a permanent one. Approximately 23 000 Cape fur seals may have occupied the Bird Island group before European exploitation. The current population for the Eastern Cape coast is considerably less than its historical size.

INTRODUCTION

Fur-seal harvesting is one of the oldest 'fisheries' in South Africa. The first known commercial sealers were the Dutch who killed *c.* 45 000 Cape fur seals near the Cape of Good Hope in 1610 (Hart, 1957; Shaughnessy, 1984). Soon after European settlement of the Cape in 1652, most of the seals in and around Table Bay were destroyed (Rand, 1950, 1972; Shaughnessy, 1984). In the late 18th and early 19th centuries operations intensified when British and American sealers began to exploit west coast seal herds (Morrell, 1832; Allen, 1899; Rand, 1950, 1972; Best & Shaughnessy, 1979; Shaughnessy, 1984). By the turn of the 20th century, Cape fur seals were almost exterminated (Anonymous, 1907). At least 23 seal colonies had been destroyed; population size of the Colonial Islands (islands of the former Cape Colony) was reduced to *c.* 20 000 (Anonymous, 1907; Shaughnessy, 1984).

The first legal protection was afforded to Cape fur seals in 1893 (ARGGI, 1894). Numbers have increased greatly since the 1940s; a response of a species recovering from over-exploitation (David, 1995). Today, 1.5 to 2 million Cape fur seals breed at 25 colonies distributed from Black Rocks (Algoa Bay) on the south-east coast of South Africa, to Cape Cross (Namibia) (Butterworth & Wickens, 1990). In 1990, seal harvesting in South Africa was suspended indefinitely, pending further research. The last harvests took place in 1989 (Wickens *et al.*, 1991). Harvesting continues in Namibia.

Knowledge of past exploitation regimes can be useful when analysing the current distribution and abundance patterns of animal populations. Currently, detailed information on the commercial exploitation of Cape fur seals is only available for seven colonies off southern Africa: Hollams Bird, Long, Albatross, Sinclair and Elephant Islands on the west coast; Seal Island in False Bay and Seal Island in Mossel Bay on the south coast (Shaughnessy, 1982, 1984). The extent of sealing operations on the Eastern Cape coast and its impact on the population is not known (Ross, 1971; Rand, 1972; Shaughnessy, 1982).

The present paper provides a review of the former distribution and abundance of Cape fur seals off the Eastern Cape coast of South Africa based on available historical records. It identifies the distribution of Eastern Cape seals before commercial sealing began; documents sealing activities off the Eastern Cape coast during the 19th and 20th centuries, and discusses current population trends in relation to past exploitation regimes. The importance of the Eastern Cape population is discussed in relation to the total population.

MATERIALS AND METHODS

Historical records

Historical information on the distribution of Eastern Cape seals was obtained from reports compiled by ships' captains, shipwrecked sailors and sealers, i.e., early sighting data. Historical information concerning sealing operations, island lease, protective legislation and skin exports, was obtained from *Records of the Cape Colony* (1812–1831); *The Cape of Good Hope Blue Books* (1821–1884); *The Cape of Good Hope Almanacs* (1830–1886); *The Eastern Province Herald* (1845–1909); *Annual Reports for the Government Guano Island* (1857–1951); The Bird Island Lighthouse Logbook from 1881 to 1967 (unpubl.); *The Cape of Good Hope Statistical Registers of the British Colonial Office* (1886–1909); *Official Year Book of the Union of South Africa and of Basutoland, Bechuanaland Protectorate, and Swaziland* (1910–1953); and The Daily Diaries of Mr. D. B. Price, formerly Chief Inspector, Government Guano Islands Division, 1938 to 1972 (unpubl.). Skin export records were used as a minimum estimate of harvesting. Total harvest figures are not known, i.e., some skins were unsuitable for export; a small percentage of skins were sold locally.

Estimate of seal numbers on the Bird Islands, Algoa Bay, before commercial exploitation began

The Birds Islands of Algoa Bay comprise Bird, Seal, Stag and Black Rocks. The number of Cape fur seal pups that occupied the Bird Island group before commercial sealing began was estimated following methods described by Crawford and Best (1990). Mean pup density was assumed to be *c.* 0.53 pups/m^2, based on mean pup counts calculated from six well established seal colonies off South Africa for which surface areas were available (Crawford & Best, 1990). Assumed pup density was multiplied by surface area measurements of the Bird Islands taken from Rand (1963, 1972). The estimated number of pups derived from this calculation was then multiplied by five to obtain an estimate of the total population (Wickens & Shelton, 1992). Original colony area included the whole above-water area, minus areas in which seals were not likely to occur, i.e., probable seabird nesting sites on Seal and Stag Island.

Pup mortality in relation to storms at Black Rocks, Algoa Bay

For this study, a weather station was established on Bird Island *c.* 1 km east of Black Rocks seal colony. Weather (including wind speed and direction) and estimated swell height were recorded three times daily (0800 hrs, 1400 hrs, 1800 hrs) by two observers. Wind speed and direction were measured using a pressure plate anemometre. Environmental observations were recorded over four pupping seasons (i.e., November and December) from 9 December 1992 to 31 January 1996. Observations continued until the end of January because during the first 1–2 months of life, seal pups are subject to considerable risk of being washed from the rocks during storms. Cape fur seal pups cannot swim proficiently until they are several months of age.

Observations of the number of pups that stranded (dead or alive) on the mainland between Port Elizabeth and Port Alfred, and on neighbouring Bird Island, were recorded during two pupping seasons from 9 December 1992 to 31 January, 1993; and 1 November 1993 to 31 January 1994. The relationship between the frequency of storms and the number of stranded pups was examined. In the present study, a storm is defined by peak wind speeds greater than 30 knots (1 knot = 1.852 km/hr).

RESULTS

Sealing operations

Cape fur seals were valued primarily for their fine quality furs (Fig. 10(a).1). Other products included blubber oil; meat; leather from the skins of old seals; and vitamin A from the liver (Green, 1955; Shaughnessy, 1981; David, 1995). Frozen carcasses have been sold to Japanese crab fishermen as bait; dried carcasses have been used for poultry feed, and genitalia have been dried and sold in powdered form to the Far East as an aphrodisiac (Green, 1955; David, 1995).

Early sealers hunted animals opportunistically; they invaded rookeries throughout the year and slaughtered animals irrespective of sex and age class. Bulls were shot with a small-calibre rifle, whereas pups were killed by a blow to the head with a heavy club. By killing pregnant females and disturbing herds during the breeding season, many herds were destroyed. It was not until the establishment of formal legal authority over sealing (1893) that harvest was conducted in a more enlightened fashion, i.e., kills were mostly restricted to pups and bulls (Shaughnessy, 1982).

Winter harvest (June–September/October) was directed at first-moult animals aged between 6.5 and 10.5 months (Shaughnessy, 1982). At this stage of development, the black natal coat has been replaced with a high quality pelt that is greyish-brown dorsally with pale throat and darker belly. The underfur has reached its greatest length and the hide is free from scars (King, 1983). A small number of sub-adult and adult seals were included in the Winter harvests (Shaughnessy, 1982).

Summer harvest (late October to early December) was generally directed at adult males, commonly referred to as wigs (Shaughnessy, 1982). Wigs were targeted primarily for their blubber oil (train). Their battle scarred hides were of little commercial interest. In the early months of Summer, wigs are in prime breeding condition; oil yield is high and they are easily approached by the sealers (Rand, 1952).

Seal islands of the Eastern Cape coast

The seal islands of Algoa Bay

There are two island groups within Algoa Bay; the Bird Island group (Bird, Seal and Stag Islands; Black Rocks), and the St. Croix Island group (St. Croix Island; Jahleel and Brenton islets) (Fig. 10(a).2; Table 10(a).1; Appendix 10(a).1a–d). With the possible exception of Bird Island, these islands were once home to num-erous seals. At present, Cape fur seals are restricted to one breeding colony; Black Rocks in the Bird Island group.

Fig. 10(a).1 Cape fur seals killed by government sealers for their fine quality furs (photograph compliments of the Government Guano Islands).

Soon after ‘knock-down’, skins were removed from the carcasses to prevent the fur slipping from the hide through overheating. Furs were then washed thoroughly; spread over a beaming board and excess blubber removed; washed and salted; piled on top of each other and cured for 6–10 days; re-salted and packed into brine soaked casks for export (Jackson, 1925; Cross, 1928).

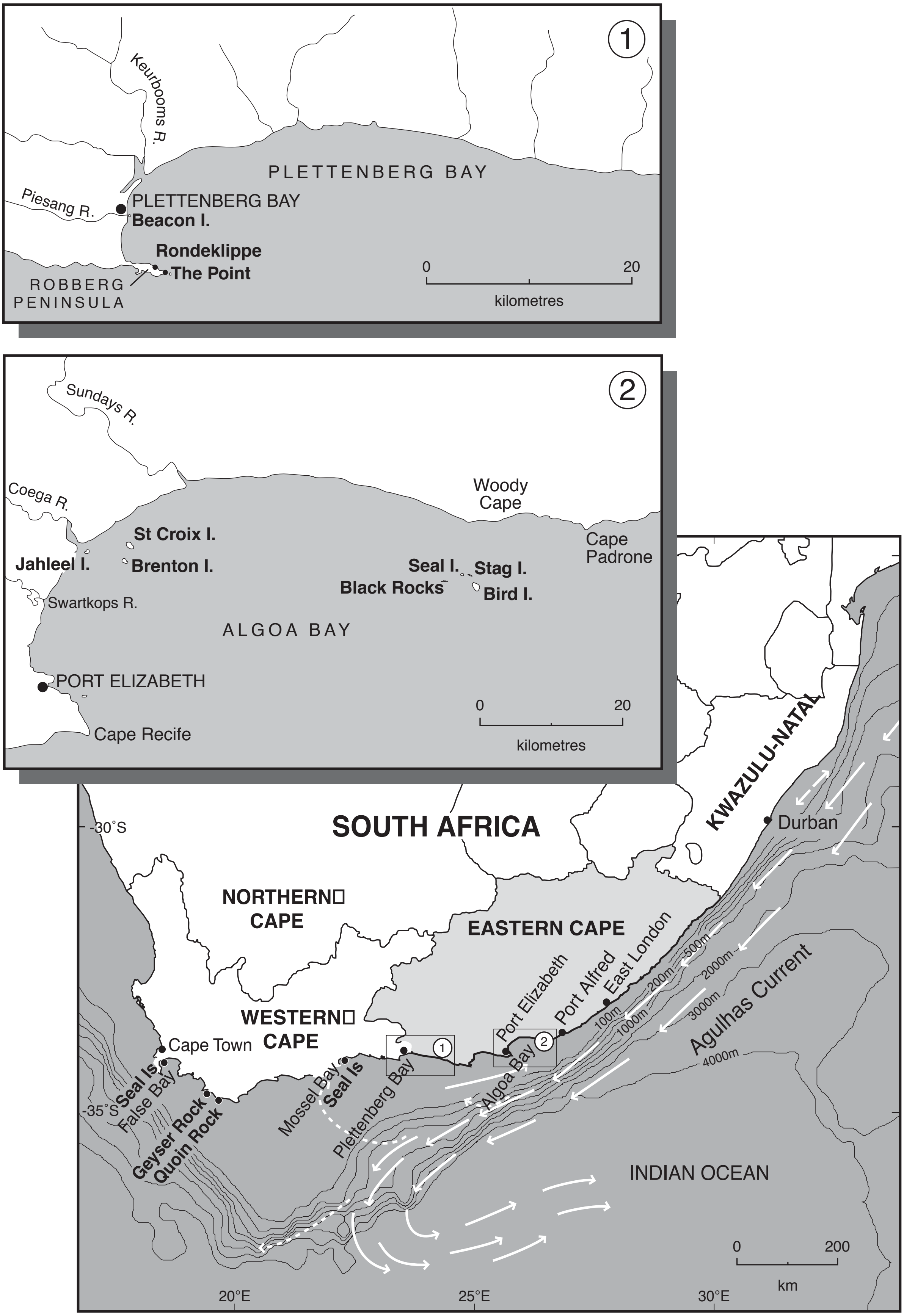

Fig. 10(a).2 The distribution of Cape fur seals along the Eastern Cape coast of southern Africa.

Before exploitation by Europeans, Cape fur seals inhabited six islands in Algoa Bay (Stag, Seal, Black Rocks, St. Croix, Jahleel and Brenton) and two sites in Plettenberg Bay (Seal Point on the Robberg Peninsula, and Beacon Island).

Table 10(a).1 *Cape fur seal colonies on the Eastern Cape coast of South Africa indicating locality and present population status*

Seal colony	Locality	Cape fur seals
ALGOA BAY		
Bird Island Group		
Bird Island	33° 50.67’S, 26° 17.34’E	unknown[a]
Stag Island	33° 50.00’S, 26° 17.00’E	extirpated
Seal Island	33° 50.00’S, 26° 17.00’E	extirpated
Black Rocks	33° 50.25’S, 26° 15.87’E	breeding colony (*c.* 710 seals in 1997)
St. Croix Island Group		
St. Croix Island	33° 47.93’S, 25° 46.25’E	extirpated
Jahleel Islet	33° 49.08’S, 25° 45.90’E	extirpated
Brenton Islet	33° 48.33’S, 25° 42.30’E	extirpated
PLETTENBERG BAY		
Beacon Island	34° 03.62’S, 23° 22.83’E	extirpated
Robberg Peninsula		
(a) Cape Seal	(a) 34° 06.45’S, 23° 24.76’E	(a) extirpated
(b) Rondeklippe	(b) 34° 06.07’S, 23° 23.96’E	(b) non-breeding colony (48–67 seals in 1996; highly variable)

[a] Available data (e.g., survivors of the shipwrecked *Doddington* in 1755) suggest that seals were not present on Bird Island historically (Webb, 1763; Temple, 1900–1902).
[Note: there is a breeding colony at Mossel Bay (Seal Island) just beyond the western boundary of the Eastern Cape coast].

The following extracts provide evidence that Cape fur seals inhabited Seal, Stag, Black Rocks, St. Croix, Jahleel and Brenton Islands historically:

In 1575, the king of Portugal (King Sebastian) selected Manuel da Mesquita da Perestrello to conduct a detailed survey of the Cape coast. January 1576, Perestrello anchored in Algoa Bay and named it *Baia des Lobos* (=Bay of wolves [seals]) (Raven-Hart, 1967). Perestrello chose the name because of the great number of seals that he found there.

On July 17, 1755, the ill-fated vessel *Doddington* was shipwrecked off Bird Island. Records of the ordeal, kept by the First Mate Evans Jones (Temple, 1900–1902) and Third Mate W. Webb (Webb, 1763), indicate that seals inhabited Seal and Stag Islands, and were occasionally found on Bird Island.

Captain P. Hornby, of the his majesty’s ship *Stag*, charted the Bird Islands in March 1814. In a letter to his superior (Vice Admiral Tyler), Hornby noted: “*the islands abound with seals, which may be killed with ease*” (RCC, Oct 1812–Apr 1814). An account of this voyage was published by Temple (1900) which confirmed that seals were present on Seal and Stag Island, and Black Rocks: “*Bird Island is the easternmost of them and is of round form and about a quarter of a mile in extent...myriads of birds, particularly gannets and penguins, covered the isle. The next about half a mile in length, called Seal Island, and the third called Stag Island, with Black Rocks that extend from it to the westward were all covered by seals*”.

In 1820, Admiral Fairfax Moresby observed numerous seals on St. Croix, Jahleel and Brenton Islands: “*These islands are inhabited by immense numbers of seals, which at times literally cover their surface*” (Moresby, 1972).

The seal islands of Plettenberg Bay

The writings of early travellers to Plettenberg Bay indicate that seals once inhabited the point of the Robberg Peninsula (i.e., Cape Seal), and Beacon Island. At present, Cape fur seals are restricted to one non-breeding colony, Rondeklippe, on the eastern side of the Robberg Peninsula between Grasnek and Witsand (Fig. 10(a).2; Table 10(a).1).

The following extracts provide evidence that Cape fur seals inhabited the Robberg Peninsula and Beacon Island historically:

In 1488, Duarte Pachecko Pereira accompanied Portuguese navigator, Bartholomeu de Novaes, on part of his homeward voyage from the Eastern Cape coast of Africa to Portugal. During this voyage, they sailed into a bay which they named *Bahia das Alagoas* (=the Bay of the Lagoons [Plettenberg Bay]) (Storrar, 1978). Pereira noted that there was a small islet (Beacon Island) in *Bahia das Alagoas* were many seals and seabirds lived (Storrar, 1981).

In July/August 1630, a Portuguese ship *San Gonzales* was shipwrecked off Plettenberg Bay (formerly *Bahia Formosa* = the Bay Beautiful). Records of the ordeal indicate that seals were abundant on Beacon Island. Soon after the ship was destroyed, the survivors (*c.* 100) began to construct two small vessels. Numerous seals were killed on Beacon Island in the construction of these vessels, i.e., for tar they used benzoin mixed with incense and seal oil (Raven-Hart, 1967; Storrar, 1977, 1978).

In March 1816, reverend Latrobe referred to a colony of seals on Beacon Island opposite the mouth of the Piesang River, Plettenberg Bay (Ross, 1971).

In August 1833, Captain Harker, the Government Resident of Plettenberg Bay, estimated that there were 3 000 seals on the Robberg Peninsula. However, in that same year, businessman George Rex, noted: "*As for the seal fishery, in one season from September to March 146 seals were taken at Robberg, all males...Harker said he had seen 3 000 on Robberg...but other people have never seen more at a time than 200 to 300. He proposed killing no more than 1 500 in a season, leaving the remaining 1 500 to breed, but having hitherto caught none but males, it would seem that it is not their breeding place*"(Metelerkamp, 1955).

Nineteenth century sealing: Algoa Bay

Soon after British settlement of Algoa Bay in 1820 (Chase, 1967, 1969), the St. Croix and Bird Islands were leased to individuals by the governor of the Cape Colony (Lord Charles Sommerset) at an annual rental, for fishing and sealing purposes (RCC, Apr–Jun 1825, Feb–Jun 1826, Dec 1827–Apr 1831; CGHBB, 1831; ARGGI, 1886). In 1822, more than 17 000 seals were killed on the Bird Islands (Table 10(a).2). Large numbers of seals were also taken from the St. Croix Islands (Settlers, 1823; RCC, Jun–Aug 1825; Moresby, 1972). Estimated population size before European exploitation would have exceeded 20 000 (present study).

The first shipment of seal skins, from Port Elizabeth (Algoa Bay) direct to London, was reported in 1831 (Chase, 1967). In 1833, regulations were intro-duced to ban foreign vessels (non-British) from sealing (and whaling) in the Cape settlement over which her British majesty had sovereignty (ALMANAC, 1833, 1837, 1842). Seal skins and blubber oil were required to be declared as British takings in order to be admitted to England (ALMANAC, 1835, 1851). Seal skins were exported regularly from Port Elizabeth until 1876, with a minimum of 2 935 skins exported between 1831 and 1850; and *c.* 3 516 between 1851 and 1876 (Table 10(a).3, 10(a).4). The average number of seal skins exported during this period was *c.* 150 per year. A maximum of 681 skins was exported in 1835.

Eyes witness accounts of seals on the Bird Islands indicate that seals remained on Black Rocks throughout the 1800s, but were greatly reduced on both Seal and Stag Islands (CGHBB, 1853–1859; Graham's Town Journal, 12 June, 1834; Pinchin, 1871; EPH, 27 September, 1878). There is evidence to suggest that Seal and Stag Islands were possibly devoid of seals during the late 1850s, 1860s and 1870s (CGHBB, 1859; Pinchin, 1871). The Stag Island population was presumably extirpated in the mid to late 1800s. During the early 1900s, Stag island was used for deblubbering, preservation of pelts and oil-extraction (UGGI files; Rand, 1972).

Table 10(a).2 ***Minimum number of Cape fur seals killed on the islands of Algoa Bay (Eastern Cape coast of South Africa) between 1822 and 1825***

Date	Island	Name of sealer	No. seals killed[a]	Source
Jan 1822 to Jan 1825	St. Croix Islands	Deal Party (Charles Gurney and his team from Deal England)	NR	1
1822	Bird Islands	James Saunders King (former British naval officer)	*c.* 3 000	2
27 June 1822 to 27 June 1825	Bird Islands	Frederick Korsten (former Dutch naval officer)	14 000[b]	3, 4
12 Dec 1823 to 9 Jan 1824	St. Croix Islands & Bird Islands	Master John Alexander (unlicensed sealer)	1 232	4

NR, not recorded.
[a] Minimum number of seals killed.
[b] 14 000 seals were killed on the Bird Islands by Korsten in a single season.
1. Settlers (1823); 2. RCC (Oct 1824–Feb 1825); 3. Chase (1969); 4. RCC (Jun–Aug 1825).

Table 10(a).3 ***Annual rental of the Algoa Bay islands and the minimum number of Cape fur seal skins exported from Port Elizabeth between 1830 and 1850.*** **Percentage of total exports from the Cape Colony is given in brackets (see Appendix 10(a).2).**

Year	**No. of skins exported from Port Elizabeth**[a] **(% of total exports)**	**Annual rent** **Bird Islands**	**Annual rent** **St. Croix Islands**	**Source**
1831	93 (1%)	–	–	CGHBB (1832) ALMANAC (1833)
1832	–	–	–	ALMANAC (1834)
1833	–	–	–	CGHBB (1833)
1834	417 (9%)	–	–	CGHBB (1834)
1835	681 (15%)	20	187	CGHBB (1835)
1836	345 (6%)	20	187	CGHBB (1836)
1837	105 (2%)	20	187	CGHBB (1837) ALMANAC (1839)
1838	44 (2%)	20	187	ALMANAC (1840)
1839	–	20	187	CGHBB (1839)
1840	111 (100%)	20	31	CGHBB (1840)
1841[b]	348 or 121	33 (J. Norton)	31	ALMANAC (1843) CGHBB (1841)
1842	348 (100%)	33 (J. Norton)	31	CGHBB (1842)
1843	159 (16%)	33 (J. Norton)	31	CGHBB (1843) ALMANAC (1845)
1844	94 (5%)	33 (J. O. Smith)	31	CGHBB (1844) ALMANAC (1846)
1845	166	33 (govt/Smith)	31	ALMANAC (1847) CGHBB (1845)
1846	0	33 (govt/Smith)	31	CGHBB (1846)
1847	139 (11%)	0 (govt/Smith)	31	ALMANAC (1849)
1848	0	0 (govt/Smith)	–	ALMANAC (1850)
1849	112 (18%)	0 (govt/Smith)	–	ALMANAC (1852)
1850	0	0 (govt/Smith)	–	ALMANAC (1853)
Total	**2 935**			

[a] Seals exported from Port Elizabeth were taken from the Bird Islands and the St. Croix Islands.
[b] Conflicting records of the number of seal skins exported (minimum value for 1841 was used to calculate the total number of skins exported).

Apart from the indiscriminate sealing operations, human activity in the area contributed to the decline in seal numbers. From the 1840s to the mid 1980s, Bird Island was managed for the pro-duction of seabird guano (Cape of Good Hope Government Gazette, 10 May 1844; Graham's Town Journal, 25 April 1844, 22 May 1845; ARGGI, 1886; Ross *et al.*, 1988). The presence of guano workers; noise created from scraping and loading guano; and the presence of small guano boats in the area, altered seal behaviour and habitat use....“*since vessels have taken guano from the Bird Islands, the seals have left*” (CGHBB, 1859).

Records suggest that seals were extirpated from the St. Croix Islands by the late 1850s; the last record of seals being killed on St. Croix was in 1858 (CGHBB, 1831–1859). During the 1860s, a whale fishery was presumably established at the St. Croix Islands (EPH, 19 August 1864); therefore, if any seals had survive, they would have been removed when the station was established. From at least 1871 to 1893, the islands were used by the government as a quarantine station, and leased under certain stipulations for fishing purposes and seabird egg collection (ADLCC, 1886–1897). In 1895, St. Croix Island was used solely as a lookout station during the whaling season (May to December); whaling boats could be stored there during the Winter months (ADLCC, 1886–1897).

Nineteenth century sealing: Plettenberg Bay

There are no official records of commercial sealing in Plettenberg Bay until 1840 (CGHBB, 1840); however, it is likely that the boats from the early whale fisheries were used to kill seals along the east coast during the late 1700s and early 1800s. The Southern Whale Fishery was established in Plettenberg Bay in 1795/6, soon after British settlement of the Bay (see Chase, 1967; Storrar, 1978).

Table 10(a).4 *Number of casks of seal skins exported from Port Elizabeth (Eastern Cape coast of South Africa) between 1851 and 1900*

Vessel	Date sailed	No. casks of skins	Estimated no. skins[a]	Source[b]
Phoenix	1851	8	600	5 July 1851 (EPH)
Victory	11 Feb 1853	2	150	15 Feb 1853 (EPH)
Ariel	1854	2	150	4 April 1854 (EPH)
Hero of the Nile	12 June 1857	2	150	16 June 1857 (EPH)
Leonidas	25 June 1859	2	150	28 June 1859 (EPH)
Maravi	3 Aug 1859	3	225	5 Aug 1859 (EPH)
Monsoon	8 May 1860	3	225	8 May 1860 (EPH)
Woodbine	14 Sep 1860	–	138	14 Sep 1860 (EPH)
Meg Merrilies	27 July 1861	8	600	30 July 1861 (EPH)
Reullura	9 Aug 1862	3	225	12 Aug 1862 (EPH)
Ariel	27 Feb 1863	3	225	3 Mar 1863 (EPH)
Veritas	20 Aug 1863	1	75	21 Aug 1863 (EPH)
Noor Jehoa	1864	2	150	26 Aug 1864 (EPH)
Arthur Pardew	14 May 1866	1	75	15 May 1866 (EPH)
Roman	11 May 1867	1	75	14 May 1867 (EPH)
Norseman	29 Feb 1868	1	75	8 March 1868 (EPH)
Good Hope	24 Oct 1868	(1 bale of skins)	?	27 Oct 1868 (EPH)
Saxson	15 March 1869	1	75	16 Mar 1869 (EPH)
Trudel	3 July 1871	1 cask (and 14 bundles of skins)	>75	4 July 1871 (EPH)
Celt	28 Aug 1872	–	3	30 Aug 1872 (EPH)
Syria	21 Dec 1873	(1 bundle of skins)	?	28 Dec 1873 (EPH)
European	29 Feb 1876	1	75	3 Mar 1876 (EPH)
Total		**45**	**> 3 516**	

[a] See Appendix 10(a).3 for calculations used to determine the estimated number of seal skins per cask.
[b] EPH, Eastern Province Herald.
[Note: there were no records of seal skin exports in the EPH after 29 February 1876].

Available records indicate that seals were occasionally killed on Robberg between 1840 and 1843, but the quantity and value are unknown (CGHBB, 1840–1843). In 1852, Robberg was leased at £5 per annum for sealing purposes; seals were killed annually between 1852 and 1857 (CGHBB, 1852–1857). There are no official records of sealing on Robberg after 1857 (CGHBB, 1858–1884; Rand, 1972).

Although it is not known when the Robberg rookery ceased to exist, it is likely that the seals were extirpated from the rookery between 1857 and 1890 (CGHBB, 1840–1857; Ross, 1971).

The Beacon Island colony survived until at least 1881. The diary of John Fisher Sewell, harbour master of Plettenberg Bay from 1875 to 1897, confirms that seals inhabited Beacon Island in the early 1880s. Sewell notes that a small seal hunt was organised on Beacon Island in 1881 (Storrar, 1981). If any seals survived until 1912, they would have been removed when a large shore whaling station was built in that year (see Kelly-Paterson, 1971; Storrar, 1978, 1981).

The Fish Protection Act of 1893

By the late 1800s, the seal population had been greatly reduced (Shaughnessy, 1984). Under the current system, the colonial government had no restriction upon the season, sex or numbers killed (ARGGI, 1894). If current sealing practices continued, "*seals would become extinct in these waters*" (as above). Thus, from 1890, the government resumed concessions for the Colonial Islands, and the first legal protection was afforded to seals in 1893 (Proclamation Number 499 of Act 15) (ARGGI, 1894). C. H. Jackson, government agent in charge of the seal and guano islands, was ordered to conserve the seals (ARGGI, 1898). From 1895 to 1909, an array of proclamations concerning sealing was introduced in an attempt to manage successfully the industry (Shaughnessy, 1984).

Twentieth century sealing: Algoa Bay

After 1893, sealing operations on the guano islands were dominated by the government; however, a limited amount of private sealing was permitted until at least 1937 (ARGGI, 1938).

Table 10(a).5 *Number of Cape fur seals killed on the islands of Algoa Bay (Eastern Cape coast of South Africa) between 1900 and 1949*

Date	Island	Name of sealer	No. seals killed	Source
July and Oct 1907	Bird Islands	NR	902 skins	1, 2
10 Sep to 17 Oct 1907	Bird Islands	Private sealing party (Robert Overstone)	> 75 skins[a]	1
1908	Black Rocks	NR	786 skins	2
5 May 1908	Bird Islands	Private sealing party (cutter *Vicking*)	NR	1
6 Nov 1911	Black Rocks	Private sealing party (Robert Bowden)	NR[b]	1
Aug and Sept 1920	Black Rocks	Private sealing party	NR	3
April 1943	Black Rocks	Government sealers	6 drums of oil	4
March 1945	Black Rocks	Government sealers	9 skins (wigs)	4
1946–1949	Black Rocks	Government sealers	546 skins (wigs)	2
Total			**> 2 318**	

NR, not recorded.

[a] 2 October 1907, Overstone borrowed 400 lbs of salt from the Bird Island lighthouse keeper to preserve his catch, i.e., enough salt for c. 75 skins (Mike Meyer, pers. comm.).

[b] 6 November 1911, the UGGI informed Oskar Larson (headman of Bird Island) that private sealer, Robert Bowden, of the cutter *Bob*, was granted a permit to seal at Black Rocks.

1. UGGI files; 2. Rand (1972); 3. BILHLB; 4. Price, D. B. (1938–1972).

Although Algoa Bay seals were hunted during the 1900s, there are no available skin export records for this period. Catch figures indicate that a minimum of 1 763 seals were killed in 1907 and 1908; and more than 500 were taken between 1943 and 1949 (Table 10(a).5).

Eyes witness accounts of seals on the Bird Islands indicate that: (i) the Stag Island population did not recover during the 1900s; (ii) a small number of seals were possibly breeding on Seal Island until at least 1909 (UGGI files; EPH, November, 1909); (iii) seals remained on Black Rocks throughout the 1900s (UGGI files; Anonymous, 1917; Fitzsimons, 1920).

In a description of the natural history of Algoa Bay, Fitzsimons (1920) reported that a large herd of seals occupied Black Rocks. Fitzsimons did not mention seals inhabiting Seal or Stag Islands, indicating that the latter colonies had been destroyed.

Although seals remained on Black Rocks throughout the 1900s, numbers were greatly reduced by the sealers. For example, in January 1912 there were only *c.* 200 adults seals and some pups on Black Rocks (UGGI files). In August 1942, the headman of Bird Island (H. Groenewald) noted... "*with regards to the killing of seals - it is very unsatisfactory...there are only a few seals...it does not seem that seal killing will be thriving here*" (UGGI files). Despite the small number of seals on Black Rocks, government sealers killed more than 500 seals during the 1940s (Table 10(a).5). All sealing operations on Black Rocks were terminated in 1949 (Rand, 1972).

Black Rocks was the only colony on the Eastern Cape coast to survive commercial sealing operations. Access to Black Rocks is difficult and for that reason sealing activities were irregular.

Table 10(a).6 *Estimated pup production of Cape fur seals on the Bird Islands (Algoa Bay) before exploitation by Europeans*

Colony	**Approximate surface area (m^2)[a]**	**Pup production**
Seal Island	6 479	2 268
Stag Island	1 129	395
Black Rocks[b]	8 360	2 926
Total		**5 586**

[a] Approximate surface areas taken from Rand (1963, 1972).
[b] This calculation refers to the main breeding rock only, i.e., the largest rocky outcrop.
[Note: pup production was estimated following methods described by Crawford & Best, 1990].

Table 10(a).7 *Population estimates for Black Rocks seal colony (Algoa Bay) based on counts of Cape fur seal pups taken from aerial photographs. All counts are for December of that year*

Year	**Seal pup count**	**Total population[a]**	**Source**
1974	904	4 520	1
1976	86	430	1
1979	442	2 210	2
1982	561	2 805	2
1986	808	4 040	2
1988	800	4 000	2
1992	463	2 315	3
1996	296	1 480	3
1997	142	710	3

[a] Total pup count multiplied by a factor of 5 (Wickens & Shelton, 1992).
[Note: see Shaughnessy (1987a) for problems associated with population estimates inferred from aerial photographs].
1. Shaughnessy (1987a); 2. Wickens & Butterworth (1990); 3. SFRI, unpubl. data.

Estimate of seal numbers on the Bird Islands, Algoa Bay, before commercial exploitation began

An estimated 23 000 Cape fur seals may have occupied the Bird Islands before exploitation began. When the total surface area of each island (Rand, 1963, 1972) is multiplied by 0.53 (Crawford & Best, 1990), pup production is *c.* 5 589 (Table 10(a).6). The total seal population is therefore 5 589 × 5 = 28 000 seals. This estimate will be considerably less when we account for those areas in which seals were not likely to occur (e.g., probable seabird nesting sites on Stag or Seal Island). For example, in the 1750s, a minimum of 500 breeding pairs of jackass penguins, *Spheniscus demersus*, occupied Seal Island, and *c.* 50 breeding pairs occupied Stag Island (Ross, 1978). Assuming that seals occupied the main rock at Black Rocks; 60–70% of Seal Island; and 50% of Stag Island, pup production is *c.* 4 598. The total population for the Bird Islands is therefore *c.* 23 000 seals. Early harvest figures support this estimate, i.e., a minimum of 17 000 seals were killed on the Bird Islands in 1822.

Only the main rock (largest rocky outcrop) at Black Rocks was included in the above calculation because it is the only one capable of supporting pups during storms with large ocean swells. Furthermore, Bird Island was excluded from the above calculation because there is no current evidence to suggest that seals have ever inhabited this island (see Temple, 1900–1902; Webb, 1763).

Current population status of Black Rocks

Available population estimates of the Black Rocks seal colony are presented in Table 10(a).7. These estimates have been inferred from aerial counts of black pups. For a number of physical reasons, aerial estimates of seal populations are negatively biased (Shaughnessy, 1987*a*, *b*).

All sealing operations on Black Rocks were terminated in 1949. By 1974, *c.* 4 500 seals inhabited Black Rocks. The population then declined to a low of *c.* 430 in 1976, and then recovered to a high of *c.* 4 000 in a ten year period (Table 10(a).7).

During the last 12 years (1986 to 1997), the population has decreased by 82%. Causes for the population fluctuations are complex. Key factors influencing this decline include: (1) impact of storms on pup survival, i.e., storm driven waves associated with *El Niño*; unusually large waves; (2) absence of seals from neighbouring Seal and Stag Islands, i.e., lack of surplus seals to repopulate Black Rocks when numbers decline after storms; and (3) interactions with commercial fisheries, i.e., by-catch and deliberate shooting of seals by fisherman (Stewardson, unpubl. data). At present, Black Rocks supports *c.* 700 seals (SFRI, unpubl. data for December 1997). The population is viable, yet vulnerable to change.

Pup mortality in relation to storms at Black Rocks, Algoa Bay

In polygynous breeding pinnipeds, such as the Cape fur seal, pups are surrounded by sexual and agonistic activity from birth; bulls intent on mating or fighting often kill or injure pups, and females may bite pups which are not their own (Rand, 1967; Wartzok, 1991). When pups are not suckling, they tend to move from the most active areas of the rookery and lie in crevices or congregate in open spaces (Rand, 1967). Where space is a limiting factor, pups may be forced to less sheltered areas were they may be washed from the rocks.

Being washed out to sea is a significant cause of pup mortality in a number of pinniped species at certain rookeries, e.g., gray seals, *Halichoerus grypus* (Baker, 1984; Anderson *et al*., 1979; Wartzok, 1991) and northern elephant seals, *Mirounga angustirostris* (Le Boeuf & Briggs, 1977). Strong currents and swells may carry pups long distances from their mothers, and the noise of the wind and surf may interfere with the ability of mothers to hear pup vocalisations (Boness *et al*., 1992; Renouf, 1984; Perry & Renouf, 1988). Unlike some species which are strong swimmers soon after birth (e.g., Bearded seals, *Erignathus barbatus*) (Burns, 1981), a young Cape fur seal is particularly vulnerable on some islands (Rand, 1967). Although Cape fur seal pups may be introduced to the water when only a few hours old, they acquire swimming abilities slowly, gaining proficiency only after some months of 'training' in the rock pools (Rand, 1967).

Space for breeding seals on Black Rocks is a limiting factor. As the number of seals increase, crowded conditions on the main breeding rock are likely to reduce the number of pups that can be successfully reared. Crowded conditions are likely to result in increased mortality. For example, when numbers are high, individuals are forced to less sheltered areas. If storms come early in the pupping season, pups inhabiting less sheltered areas are more likely to be washed from the rocks. Although low lying areas are more prone to surging swells, large swells may also break over the main breeding rock which rises to 6 metres above mean sea level (Fig. 10(a).3). The largest outcrop is the only one capable of supporting pups during heavy seas. When very large swells sweep the colony (e.g., December 1976) all pups, irrespective of their location, may be washed from the rocks.

Before commercial sealing began, seals were plentiful on Seal and Stag Islands. When population density was high, some seals would have been forced to inhabit other sites, e.g., Black Rocks. Neighbouring islands would have played a significant role in maintaining seal numbers on Black Rocks. However, over harvesting greatly reduced seal numbers and changed distribution patterns. Seals now inhabit a single island, Black Rocks. Black Rocks may have been a 'refuge' from commercial sealers, but provides little protection against storms. When storm induced pup mortality is high on Black Rocks, there is no recruitment from neighbouring islands (i.e., extirpated), thus recovery is a gradual process. The intensity and frequency of storms during the pupping season is a key factor influencing population fluctuations at Black Rocks. By destroying seal herds through commercial harvesting, and confining the population to Black Rocks, the population is unable to build up its numbers sufficiently to stimulate colonisation on neighbouring islands.

Weather data collected from the Bird Island weather station (Table 10(a).8, 10(a).9) indicates that wind waves (waves produced by local prevailing wind), and swell waves (wind-generated waves which have moved away from their source area, independent of the prevailing wind) can have a negative influence on seal pup survival. Of the 28 strandings recorded during the 1992–1993 and 1993–1994 pupping season, 75% were associated with wind speeds 20 to 30 knots or greater, and swell height ≥ 1.5 metres (Table 10(a).10). Considering that many of the pups washed from the rocks would have drowned or have been eaten by sharks, and a percentage of those that made it ashore may have been missed by observers or scavenged, overall pup mortality would have been much higher.

Unusually large swell waves (≥ 4 metres) during the pupping season were not recorded in the present study; however, swell ≥ 4 metres was responsible for mass strandings (i.e., 50–300 pups) in December

Fig. 10(a).3 South-westerly swell breaks over the Black Rocks seal colony (Algoa Bay).
When wind waves and/or swell waves flood nursing habitat, pup mortality can be substantial.

1974, December 1976, January 1986; and possibly in December 1977 and December 1987 (Stewardson, 1999; Appendix 10(a).4). Three of these mass strandings occurred during warm phase El Niño years, i.e., 1976, 1986 and 1987 (see Mariner, 1998). Storm driven waves associated with El Niño have resulted in dramatic pup losses elsewhere (e.g., LeBoeuf & Condit, 1983; Ono *et al*., 1987).

The importance of the Eastern Cape population in relation to the total population

The majority of Cape fur seals occur on the west coast, in nutrient rich waters of the Beunguela Current. The remainder of the population (less than 10%) inhabit the south and south-east coasts, between False Bay and Algoa Bay at six colonies (David, 1995). Three of these colonies (Geyser Rocks, Quoin Rock and Seal Island-False Bay) occur in the west of the Agulhas/Atlantic mixing area and three (Seal Island-Mossel Bay; Rondeklippe-Plettenberg Bay; Black Rock-Algoa Bay) in the east, inshore of the warm Agulhas Current (Rand, 1967; Shannon, 1989). The distribution of the population is associated with the productivity of these three coastal zones. Compared with the west coast, the Eastern Cape coast population is a marginal one.

It is unlikely that the south coast and south-east coast seal populations will increase greatly because the seal islands are small in size (limited space for breeding seals) and the waters are warm (reduced productivity compared with the west coast). As global warming increases and sea levels rise, suitable habitat (small rocky islands) will be reduced. Seals will be forced to find mainland breeding colonies. However, as human activities intensify, factors such as human presence, noise, and physical habitat alteration, limit the number of potential sites.

A more immediate threat to the seal population off the southern coast is interaction with the commercial fishing industry. As the number of trawlers increase, the potential of seals being caught incidentally in fishing gear and killed is also increased (Stewardson, unpubl. data). Furthermore, seals and the industry compete for commercially

Table 10(a).8 ***The number of recording periods during which strong winds (≥ 28 knots) were noted at the Bird Islands (Algoa Bay).*** **Observations were made thrice daily (0800 hrs, 1400 hrs and 1800 hrs) during four pupping seasons, from 1 November to 31 January, 1992 to 1996.**

Pupping season	**No. of recording periods with local winds ≥ 28 knots**			
(Nov, Dec & Jan)	**NW–NE**	**ENE–ESE**	**SE–SW**	**WSW–WNW**
1992/1993[a]	0	2	2	1
1993/1994	0	2	3	2
1994/1995	0	1	1	2
1995/1996	0	3	0	0
Total	**0**	**8**	**6**	**5**

[a] For the purpose of this study, the 1992/1993 season commenced 9 December 1992, when the weather station was established. [Note: one recording period is 0800 hrs or 1400 hrs or 1800 hrs].

Table 10(a).9 ***Swell height and wind direction recorded thrice daily (0800 hrs, 1400 hrs and 1800 hrs) at the Bird Islands (Algoa Bay) during four pupping seasons, from 1 November to 31 January, 1992 to 1996***

Pupping season	**Swell height (metres)**				**Wind direction (%)[a]**			
(Nov, Dec & Jan)	**≤1**	**1.5–2**	**2.5–3**	**3.5–5**	**N**	**E**	**S**	**W**
1992/1993[b]	104	51	5	0	4	27	49	17
1993/1994	259	17	0	0	5	41	25	28
1994/1995	98	130	39	9	4	34	29	33
1995/1996	68	111	81	16	5	38	22	34

[a] Wind direction was not recorded for 5 periods during the 1992/1993 season, 1 period during the 1994/1995 season and 1 period during the 1995/1996 season.
[b] For the purpose of this study, the 1992/1993 season commenced 9 December 1992, when the weather station was established. [Note: one recording period is 0800 hrs or 1400 hrs or 1800 hrs].

Table 10(a).10 ***Relationship between the number of stranded seal pups from Black Rocks (Algoa Bay), wind force and swell height.*** **Environmental observations were made thrice daily (0800 hrs, 1400 hrs and 1800 hrs) at the Bird Islands (Algoa Bay) during two pupping seasons, 9 December 1992 to 31 January 1993, and 1 November 1993 to 31 January 1994.**

Wind speed	**Swell height (metres)**			
(knots)	**0.5**	**1.5**	**2**	**3**
17	2	0	0	0
18	1	0	0	0
19	0	0	1	0
20	1	0	0	0
24	0	2	0	0
25	2	0	0	0
31	0	2	6	11
Total	**6**	**4**	**7**	**11**

[Note: one recording period is 0800 hrs or 1400 hrs or 1800 hrs. Stranded seal pups were observed between Port Elizabeth and Port Alfred, and on neighbouring Bird Island. These pups had been washed from Black Rocks (Algoa Bay)].

important fish, notably hake, *Merluccius* spp., anchovy, *Engraulis capensis*, pilchard, *Sardinops sagax*, and horse mackerel, *Trachurus trachurus capensis*. Overfishing may reduce the amount of food available to seals and/or change feeding patterns (e.g., Reijnders *et al.*, 1993). In recent years, there have been renewed calls from the fishing lobby for a forced reduction of the Cape fur seal population.

CONCLUSION

This is the first detailed study documenting the fur seal industry off the Eastern Cape coast of South Africa. Before commercial exploitation by Europeans began in 1610, Cape fur seals inhabited six islands in Algoa Bay (Seal, Stag, Black Rocks, St. Croix, Jahleel and Brenton) and two sites in Plettenberg Bay (Seal Point on the Robberg Peninsula and Beacon Island). By the early 1900s, all Eastern Cape colonies were extirpated, with the exception of Black Rocks. Currently, Black Rocks is comprised of *c.* 700 seals. Numbers have decreased by 82% in the last 12 years. We suggest that by destroying seal herds, and confining the population to Black Rocks, the population is unable to build up its numbers sufficiently to stimulate colonisation on neighbouring islands. Limited space for breeding seals and the influence of storms restricts the number of pups that can be reared successfully. The effect of man on the Seal, Stag and Black Rocks population is therefore a permanent one. Other anthropogenic factors, including incidental by-catch and deliberate killing of seals by fisherman, also contribute to population decline in this region (Stewardson, unpubl. data). It is unlikely that the seal populations along the southern coast will increase greatly because the seal islands are small in size, and the waters are less productive compared with the west coast. Approximately 23 000 Cape fur seals may have occupied the Bird Islands before exploitation began. The current population size for the Eastern Cape coast is considerably less than its historical size.

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1823. **CO5965**, p. 190–223.
1824. **CO5966**, p. 19–48.
1825. **CO5967**, p. 172–194.
1826. **CO5968**, p. 152a–169.
1827. **CO5969**, p. 125–146.
1828. **CO5970**, p. 180c–194.
1829. **CO5972**, p. 198a–217.
1830. **CO5973**, p. 190–295.

1831. **CO5974**, p. 195–248.
1833. **CO5975**, p. 163–215a.
1834. **CO5976**, p. 160–176.
1835. **CO5977**, p. 151–176a.
1836. **CO5978**, p. 151–176a.
1837. **CO5979**, p. 159–168.
1838. **CO5980**, p. 147–156.
1838. **CCP9/1**, p. 259–263.
1839. **CCP9/2**, p. 261–269.
1840. **CCP9/3**, p. 299–301.
1841. **CCP9/4**, p. 293–295.
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1842. **CCP9/5**, p. 274, 297–299.
1843. **CCP9/6**, p. 276, 297–299.
1844. **CCP9/7**, p. 312, 347.
1845. **CCP9/8**, p. 318, 353.
1846. **CCP9/9**, p. 374, 391, 395.
1847. **CCP9/10**, p. 376, 391, 395 (also see 399).
1848. **CCP9/11**, p. 428, 447, 451, 453.
1849. **CCP9/12**, p. 446, 467, 469.
1850. **CCP9/13**, p. 444, 463, 467, 469.
1851. **CCP9/14**, p. 444, 471 (also see 463, 467, 469).
1852. **CCP9/15**, p. 430, 456–458.
1853. **CCP9/16**, p. 430, 457–459.
1854. **CCP9/17**, p. 452, 481–483.
1855. **CCP9/18**, p. 500, 531–533.
1856. **CCP9/19**, p. 525, 553–555.
1857. **CCP9/20**, p. BB7, BB9, v82, v88, v94.
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1859. **CCP9/22**, p. AA86, AA92, FF13.
1860. **CCP9/23**, p. AA81, AA86, FF13.
1861. **CCP9/24**, p. AA74, AA79, FF13.
1862. **CCP9/25**, p. AA77, AA81, FF13.
1863. **CCP9/26**, p. AA70, AA75, FF13.
1864. **CCP9/27**, p. AA68, AA73, FF13.
1865. **CCP9/28**, p. AA68, AA72, FF13.
1866. **CCP9/29**, p. AA66, AA70, FF13.
*Manufactures, Mines & Fisheries; Shipping and Imports and Exports 18***:
1867. **CCP9/30**, p. AA62, AA66, FF13.
1868. **CCP9/31**, p. AA62, AA65, FF3.
1869. **CCP9/32**, p. AA65, AA68.
1870. **CCP9/33**, p. AA67, AA71, FF3.
1871. **CCP9/34**, p. AA73, AA78, FF3.
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1875. **CCP9/38**, p. AA37.
1876. **CCP9/39**, p. T70.
1877. **CCP9/40**, p. N35.
1878. **CCP9/41**, p. N21.
1879. **CCP9/42**, p. N23.
1880. **CCP9/43**, p. Na21.
1881. **CCP9/44**, p. Na24.
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1890. **10/5**, p. 140, 173.
1891. **10/6**, p. 141, 173.
1892. **10/7**, p. 183.
1893. **10/8**, p. 176.
1894. **10/9**, p. 186.
1895. **10/10**, p. 186.
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1903. **10/18**, p. 221.
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1937. **7/33**, p. 977, 978.
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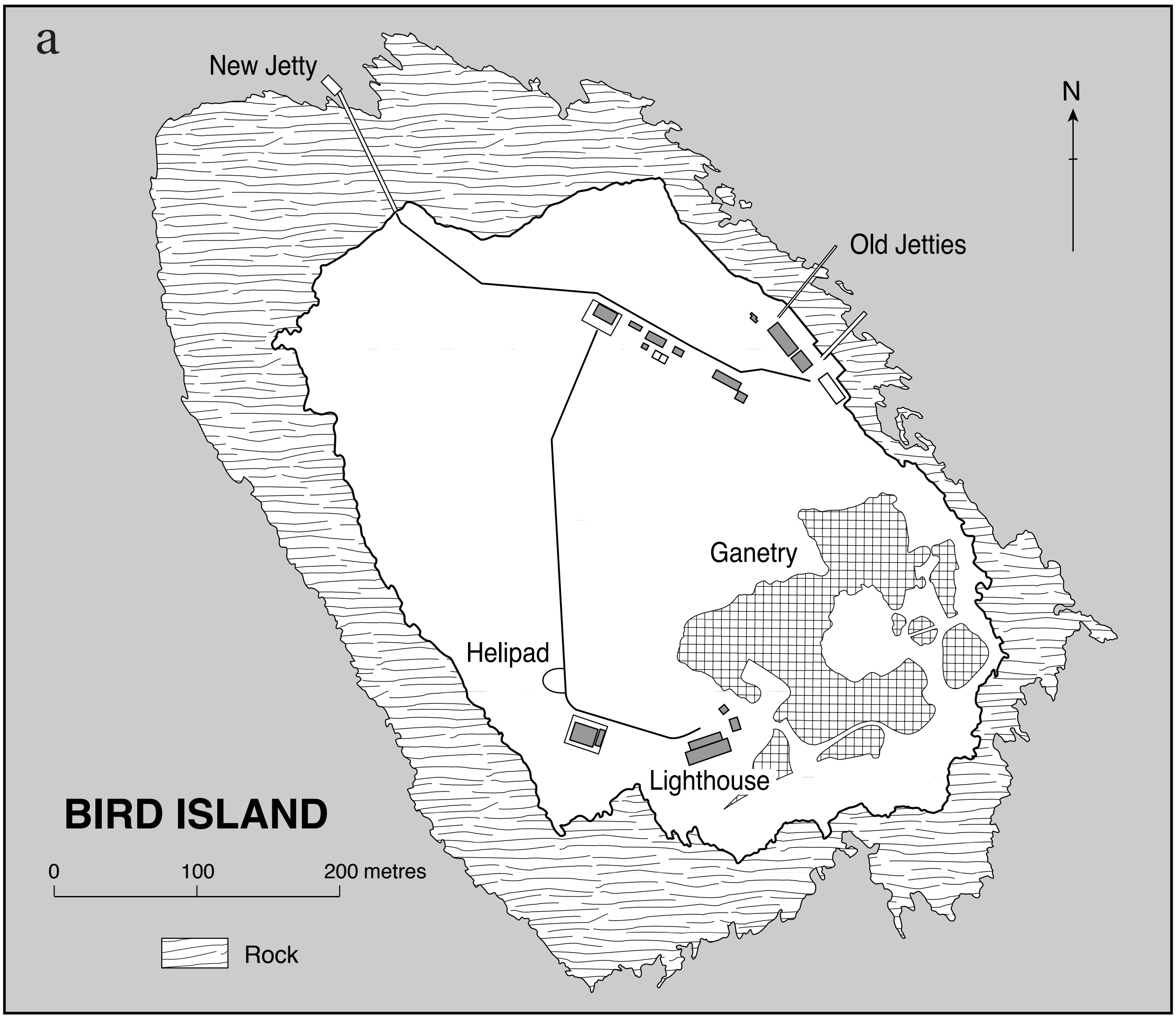
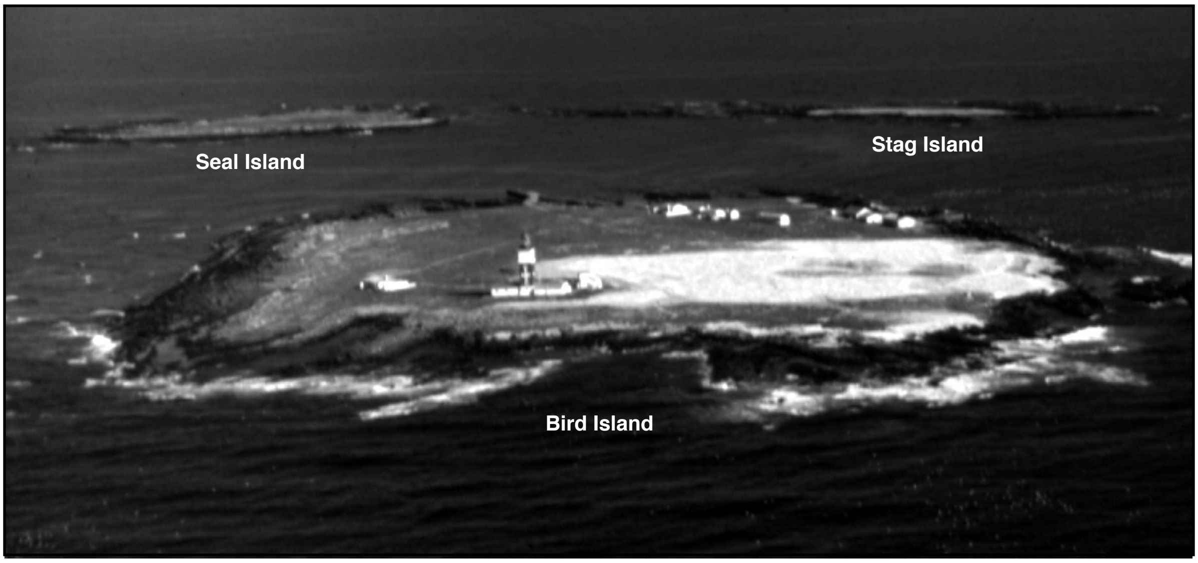
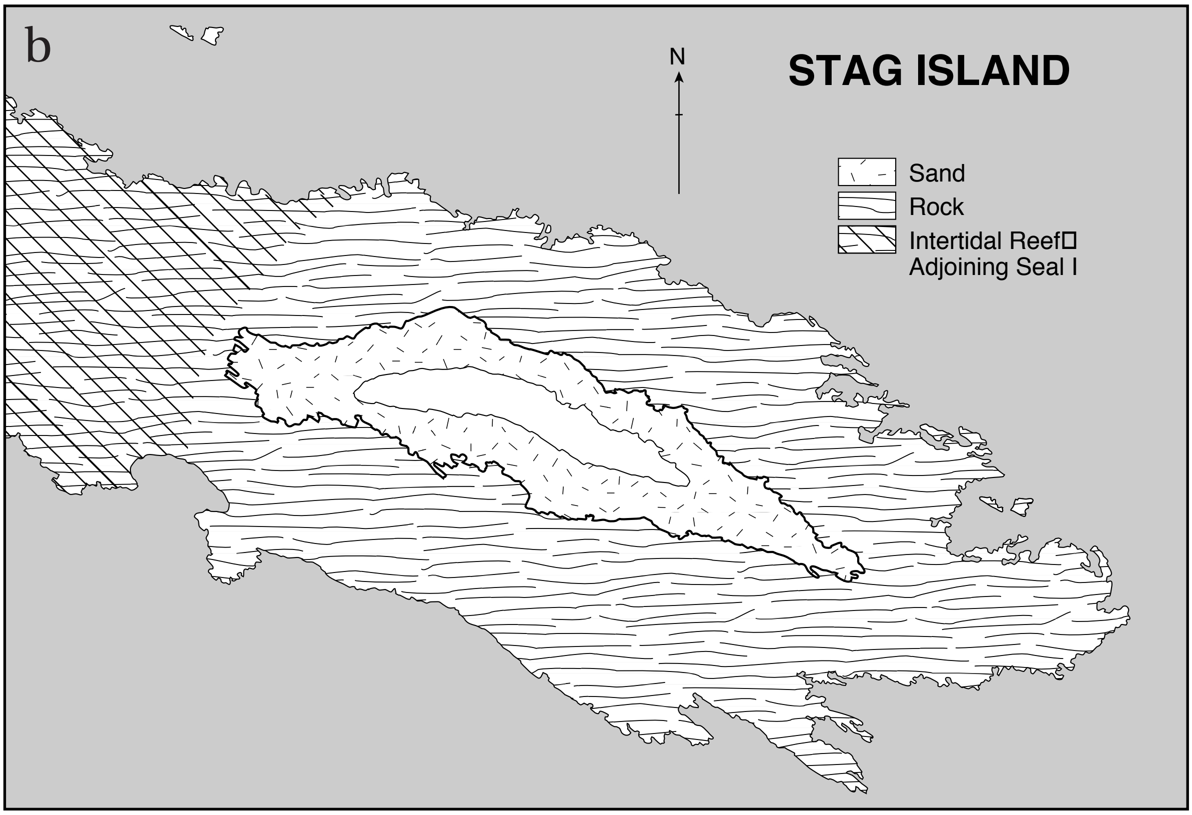
Appendix 10(a).1 ***The Bird Island group (Algoa Bay): a. Bird Island, b. Stag Island, c. Seal Island and d. Black Rocks.*** **Aerial photographs taken in April 1994 by C.L. Stewardson.**





[Note: Accurate ground measurements were not available for Seal and Stag Island or Black Rocks, therefore it was not possible to provide a scale for three of the four maps].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STAG ISLAND
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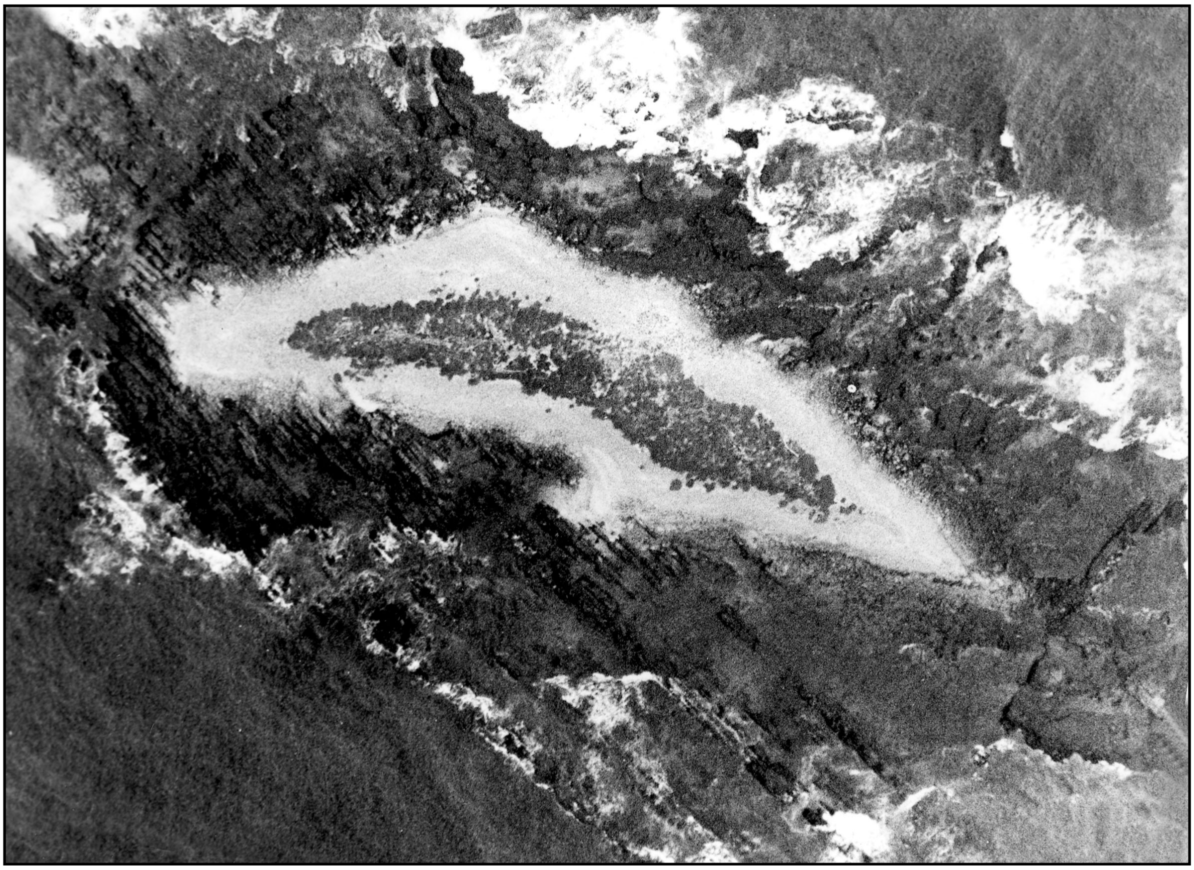
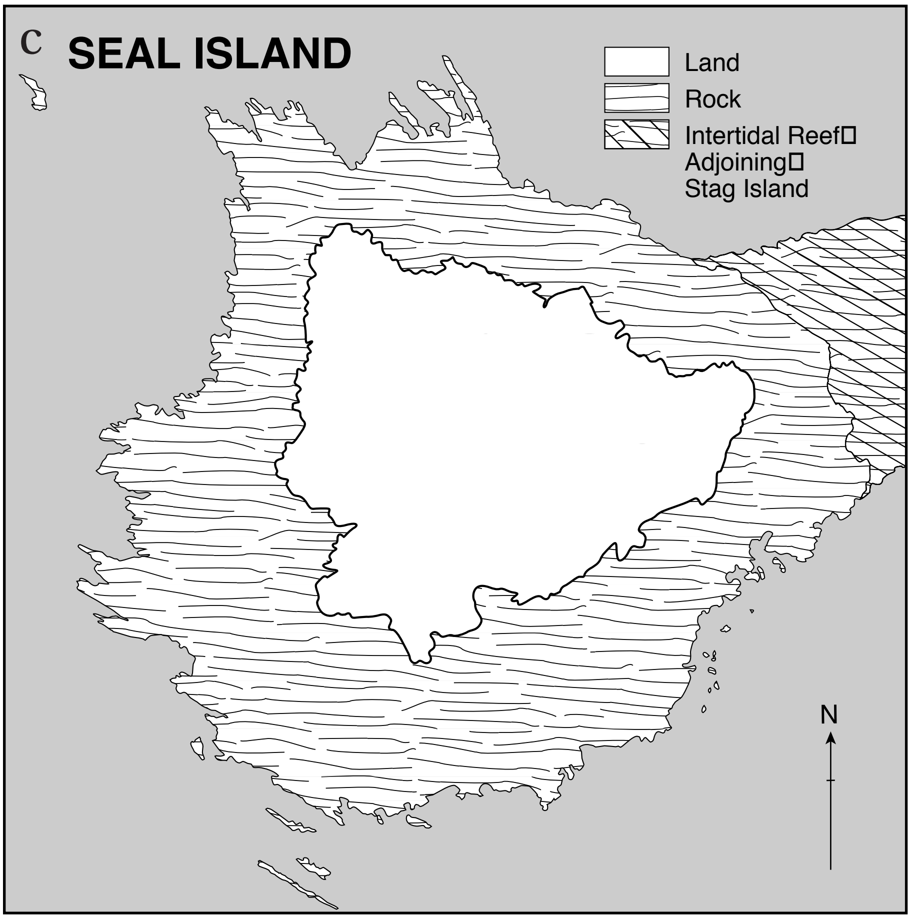
Rock
Intertidal Reef
Adjoining Seal I




c
SEAL ISLAND
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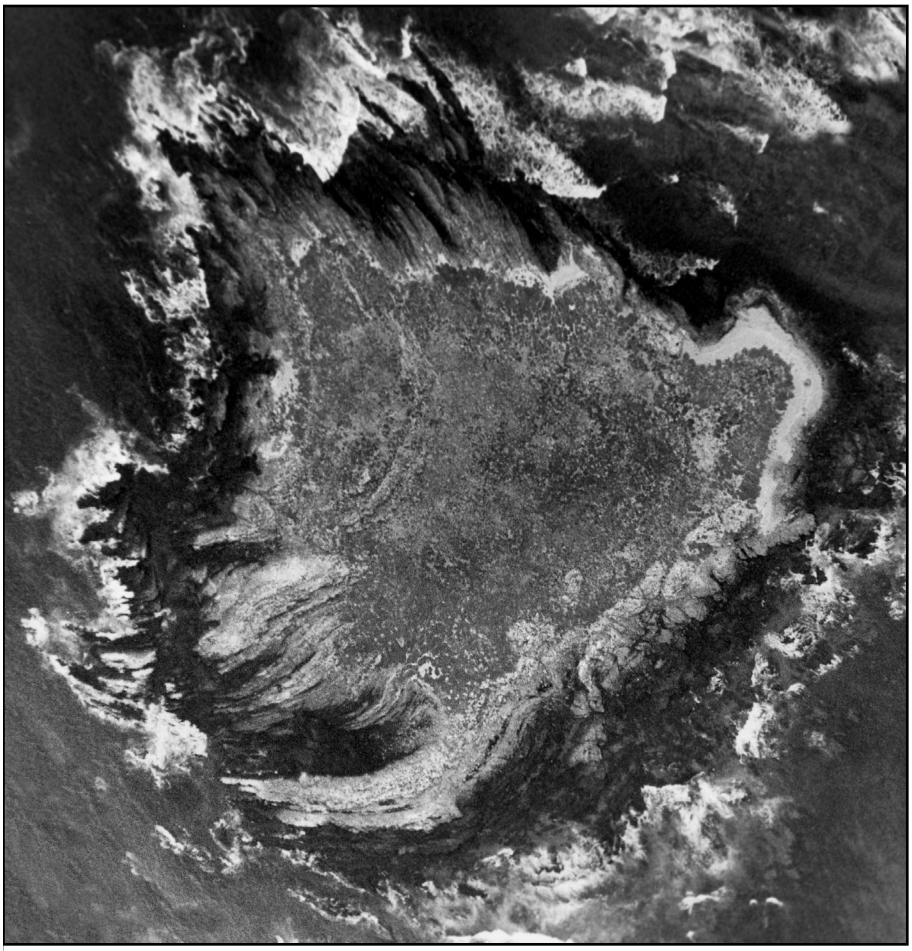

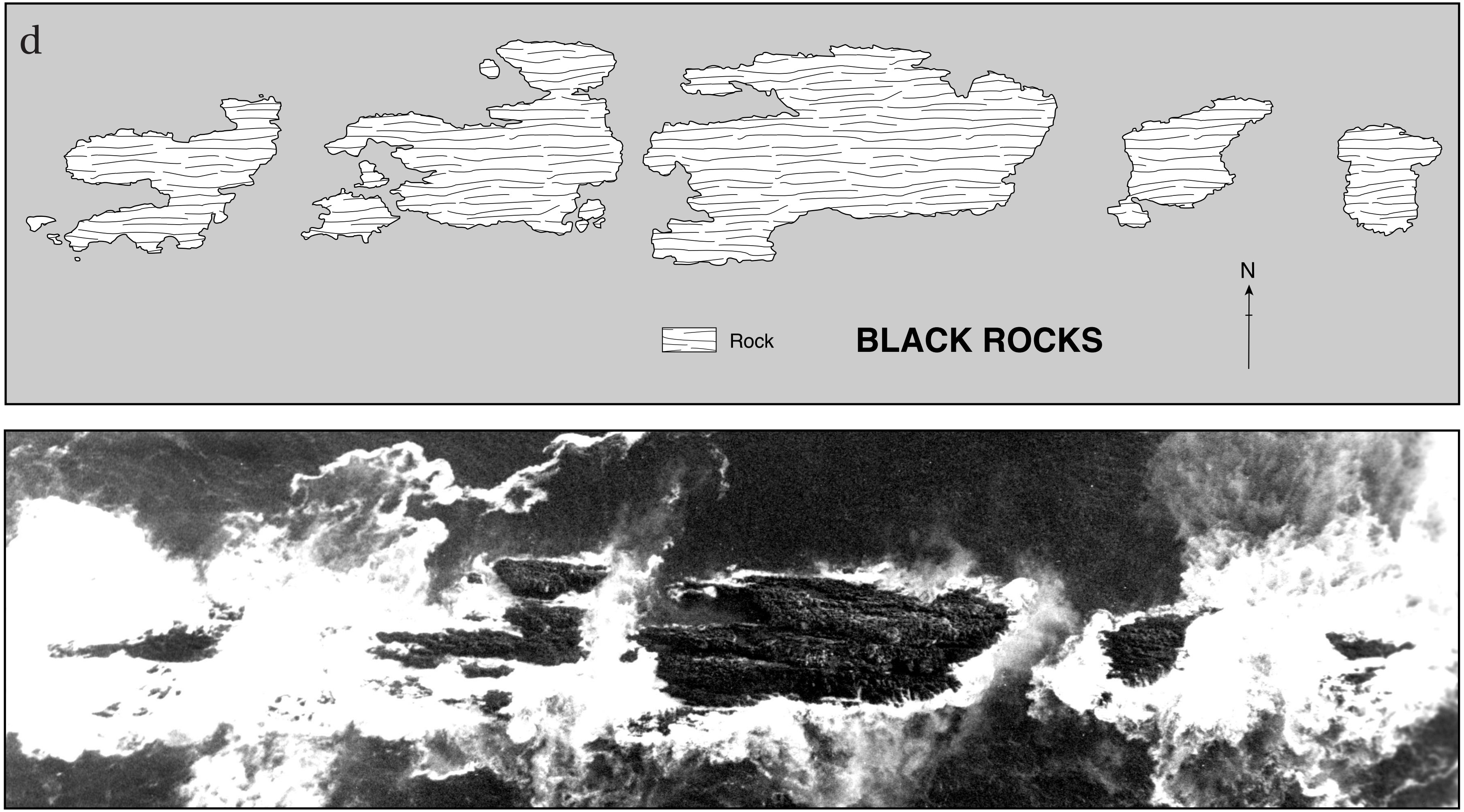
d
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Rock
BLACK ROCKS

Appendix 10(a).2 ***The number of Cape fur seal skins exported from South Africa between 1817 and 1950 according to official government registrars***

Year	No. seal skins	Value (£)	Source
1817	NR	1 900 (rands)	RCC (1826)
1818	NR	12 250 (rands)	RCC (1826)
1819	NR	3 450 (rands)	RCC (1826)
1820	NR	14 490 (rands)	RCC (1826)
1821	NR	15 920 (rands)	RCC (1826)
1822	22 625	37 700 (rands)	CGHBB (1822); RCC (1826)
1823	16 177	21 274 (rands)	CGHBB (1823); RCC (1826)
1824	6 387	14 920 (rands)	CGHBB (1824); RCC (1826)
1825	13 756	55 440 (rands)	CGHBB (1825); RCC (1826)
1826	2 408	13 146 (rands)	CGHBB (1826); RCC (1826)
1827	13 442	NR	CGHBB (1827)
1828	1 055 (pieces)	NR	CGHBB (1828)
1829[a]	3 928 (pieces) or 3 744 (skins)	834	CGHBB (1829) ALMANAC (1831)
1830[a]	5 835 (pieces) or 4 798 (skins)	940	CGHBB (1830); ALMANAC (1832)
1831[a]	9 186 (pieces) & 93 (bundles) or 9 279 (skins)	1 792	CGHBB (1832); ALMANAC (1833)
1832	3 520 (pieces)	851	ALMANAC (1834)
1833	3 582	NR	CGHBB (1833)
1834	4 947	NR	CGHBB (1834)
1835	4 644	NR	CGHBB (1835)
1836	6 489	NR	CGHBB (1836)
1837	5 384	3 855	CGHBB (1837); ALMANAC (1839)
1838	3 430	1 562	ALMANAC (1840)
1840	111	NR	CGHBB (1840)
1841	588	482	ALMANAC (1843)
1842	348	NR	CGHBB (1842)
1843	1 019	675	CGHBB (1843); ALMANAC (1845)
1844	2 202	735	CGHBB (1844); ALMANAC (1846)
1845[a]	172 or 166	93	ALMANAC (1847); CGHBB (1845)
1847	1 262	242	ALMANAC (1849)
1848	168	100	ALMANAC (1850)
1849	633	214	ALMANAC (1852)
1850	918	420	ALMANAC (1853)
1852	1 176	350	ALMANAC (1854)
1853	768	129	ALMANAC (1855)
1854	348	88	ALMANAC (1856)
1884	2 834	1 058	CGHSRBCO (1886)
1885	4 331	978	CGHSRBCO (1886)
1886	3 262	963	CGHSRBCO (1886)
1887	4 351	1 052	CGHSRBCO (1887)
1888	3 638	1 749	CGHSRBCO (1888)
1889	4 842	1 727	CGHSRBCO (1889)
1890	6 510	4 140	CGHSRBCO (1890)
1891	4 480	3 183	CGHSRBCO (1891)
1892	2 061	1 420	CGHSRBCO (1892)
1893	2 938	1 607	CGHSRBCO (1893)
1894	1 634	872	CGHSRBCO (1894)
1895	888	754	CGHSRBCO (1895)
1896	386	334	CGHSRBCO (1896)
1897	15	12	CGHSRBCO (1897)
1898	2 292	1 414	CGHSRBCO (1898)
1899	768	1 308	CGHSRBCO (1899)
1900	0	0	CGHSRBCO (1900)
1901	4 436	2 238	CGHSRBCO (1901)
1902	1 067	1 357	CGHSRBCO (1902)

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Year	**No. seal skins**	**Value (£)**	**Source**
1903	0	0	CGHSRBCO (1903)
1904	4 437	2 217	CGHSRBCO (1904)
1905	0	0	CGHSRBCO (1905)
1906	0	0	CGHSRBCO (1906)
1907	0	0	CGHSRBCO (1907)
1908	0	0	CGHSRBCO (1908)
1911	WR	2 791	OYB (1910–16)
1912	WR	3 535	OYB (1910–16)
1913	WR	5 609	OYB (1910–16)
1914	WR	2 650	OYB (1910–16)
1915	WR	845	OYB (1910–16)
1916	WR	215	OYB (1910–16)
1917	WR	4 279	OYB (1910–17)
1918	WR	4 710	OYB (1910–18)
1919	WR	8 951	OYB (1910–20)
1920	WR	15 933	OYB (1910–20)
1921	WR	12 111	OYB (1910–21)
1922	WR	14 034	OYB (1910–22)
1923	WR	14 507	OYB (1910–24)
1924	WR	17 456	OYB (1910–25)
1925	WR	17 557	OYB (1926–27)
1926	WR	13 174	OYB (1926–27)
1927	WR	11 577	OYB (1927–28)
1928	WR	16 927	OYB (1928–29)
1929	WR	14 035	OYB (1929–30)
1930	0	0	OYB (1930–31)
1931	0	0	OYB (1931–32)
1931	0	0	OYB (1931–32)
1932	0	0	OYB (1932–33)
1933	WR	2 570	OYB (1933–34)
1934	WR	2 845	OYB (1934–35)
1935	WR	20	OYB (1937)
1936	2 689	1 630	OYB (1938)
1937	14 453	8 113	OYB (1938–39)
1938	11 756	NR	OYB (1940)
1939	WR	5 048	OYB (1939)
1940	0	0	OYB (1941)
1945	7 009 & 4 298	25 103 & 63 519	OYB (1948)
1946	8 526 & 5 008	31 508 & 81 674	OYB (1948)
1947	9 507 & 6 568	37 621 & 107 694	OYB (1948)
1948	3 594 & 3 956	20 571 & 65 649	OYB (1948)
1949	6 373 & 3 372	NR	OYB (1952–53)
1950	10 986 & 1 883	NR	OYB (1952–53)

These figures were used to compare the number of seal skins exported for Port Elizabeth to the total number of seal skins exported from the Cape Colony, i.e., % of total exports, Table 10(a).3.

[a] Records give conflicting export figures.

WR, weight recorded, i.e., seal skin exports reported by weight only.

[Note: little information is available from 1855 to 1883, and from 1941 to 1944. Thus, this table must be regarded as the minimum number of seal skins exported].

Appendix 10(a).3 *Estimated number of Cape fur seal skins per cask*

No. of casks	No. of skins	Estimated no. of skins per cask	Date	Source
63	4 925	78	14 August 1823	3
17	1 200	71	1 September 1957	1
20	1 336	67	3 October 1959	1
46	3 411	74	22 October 1963	1
19	1 453	76	13 December 1963	1
37	2 863	77	8 October 1964	1
10	748	75	26 August 1965	1
20	1 258	63	29 October 1965	1
35	2 523	72	25 September 1966	2
16	1 164	73	15 August 1967	1
7	544	78	22 August 1967	1
11	856	78	29 August 1967	1
14	1 166	83	29 August 1967	1
10	687	69	29 August 1967	1
14	1 078	77	9 August 1968	2
16	1 184	74	23 August 1968	1
14	1 077	77	25 August 1968	1
4	329	82	26 August 1968	1
28	2 126	76	22 September 1968	1
28	2 169	77	21 September 1968	1
11	789	71	27 July 1969	1
6	403	67	27 July 1969	1
4	284	71	7 August 1969	1
13	890	68	7 August 1969	1
18	1 264	70	11 August 1969	1
16	1 201	75	15 August 1969	1
26	1 924	74	4 September 1969	1
23	1 431	62	7 September 1969	1
41	3 311	81	1 October 1969	2
15	1 197	80	27 October 1969	2
20	1 444	72	3 August 1970	2
38	2 342	62	30 October 1970	1
40	3 123	78	6 November 1970	1
5	398	80	4 December 1970	2
66	4 651	70	24 October 1971	1
12	920	77	11 October 1972	1
12	940	78	12 October 1972	1
13	1 034	80	16 October 1972	1
15	1 250	83	18 October 1972	1
12	976	81	20 October 1972	1
13	1 029	79	24 October 1972	1
8	656	82	26 October 1972	1
10	775	78	27 October 1972	1
13	924	71	31 October 1972	1
24	1 809	75	13 November 1972	1
13	887	68	16 November 1972	1
Mean ± S.D. **(*n* = 46)**		**75 ± 5.46**		

Estimates were made from available records for which the number of skins and the number of casks were known.
1. Price (1938–1972); 2. Miles (1966–1971); 3. RCC (June–August 1825) p. 410.

Appendix 10(a).4 *Evidence of mass strandings of Cape fur seal pups attributed to storms*[1] *at Black Rocks, Algoa Bay*

10 January 1912 Headman of Bird Island (O. Larson) to the UGGI... "*A lot of pups have been washed ashore (at Bird Island) during strong north-westerlies*" (UGGI files).

31 December 1948 Headman of Bird Island (H. J. Groenwald) to the UGGI... "*We had a strong south-westerly wind with a stormy sea. A whole lot of seals climbed out here (Bird Island) and quiet a few have been noticed moving with the stream past here*" (UGGI files).

29 December 1974. "*Hundreds of stranded seals pups were sighted along the Eastern Cape coast between 31 December 1974 and 6 January 1975. Some pups were found more than 60 km from the Black Rocks*" (Ross, pers. comm.). Strong south-westerly winds of 63 kts (max. gust) were recorded at the Port Elizabeth weather station on 28 December. Swell height of 4–5 metres (west-south west) and sea height of 3 metres was recorded in the general vicinity (Area: 33–34; 26–27) on 28–29 December. Pup counts conducted on 18 December 1974 establish that there were 904 pups on Black Rocks. Counts in mid March indicate that most of these pups had perished; less than 50 pups remained (Shaughnessy, 1982).

4 December 1976 "*200–300 pups were washed ashore between Woody Cape and East London during strong gales on 4 December. Many of these pups were returned to Black Rocks by SAAF helicopters of the 16 Squadron, Port Elizabeth*" (EPH, 8 December 1976, 11 February 1977). Strong south-south westerly winds of 69 kts (max. gust) were recorded at the Port Elizabeth weather station on 4 December. Sea state records are not available for 1–4 December; however, swell height of 9 metres (west-south west) and sea height of 5 metres were recorded in the general vicinity (Area: 33–34; 26–27) on 5 December [A pictorial account of this rescue mission is held at the Cape Archives Repository, Cape Town (Stewardson, 1999)].

16 December 1977 "*Between December 16 and 20, at least 26 stranded (dead and alive) seals pups were found as far as 39 km east of Sundays River mouth. Strong winds were recorded from 13–16 December. On 20 December, SAA helicopters returned 18 live pups to Black Rocks (7 from Port Alfred, 8 from Port Elizabeth and 3 from the air search)*" (G. Ross, pers. comm.). Strong south-westerly winds of 51 kts (max. gust) were recorded at the Port Elizabeth weather station on 13 December. Sea state records are not available for this period.

2–3 January 1986 "*Fifty to 60 pups from Black Rocks were washed ashore between Port Alfred and Sundays River Mouth after south-westerly gales*" (G. Ross pers. comm.). Strong south westerly winds persisted from 28 December with all days peaking at 25 kts (average) and gusting between 35 and 50 kts on almost every day. Swell height of 4 metres (south-south west) and sea height of 1 metre were recorded in the general vicinity (Area: 33–34; 26–27) on 1 January.

27 December 1987 "*More than 200 pups were washed ashore along the coast between the Sundays River and Port Alfred...the pups had been washed ashore from Black Rocks, near Bird Island, by the strong winds....the 200 stranded pups were put down by vets*" (EPH, 5 January 1988). Strong south-westerly winds of 60 kts (max. gust) were recorded at the Port Elizabeth weather station on 27 December. Sea state records are not available for this period.

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[1] Wind information was kindly provided by Garth Samson (Port Elizabeth Weather Bureau, Port Elizabeth, South Africa) and the swell information by Dr Marten Grundlingh (Southern African Data Centre for Oceanography, Stellenbosch, South Africa).

CHAPTER 10(b)

Supplementary paper

South African Airforce wildlife rescue: Cape fur seal pups (*Pinnipedia: Otariidae*) washed from Black Rocks, Algoa Bay, during heavy seas, December 1976

C. L. Stewardson

Published (1999) in Australia by the Division of Botany and Zoology, Australian National University, Canberra ACT 0200,
Australia in association with the World Wide Fund for Nature - South Africa.
ISBN 0 7315 3318 6, pages 1–17.

This report documents a wildlife rescue operation along the Eastern Cape coast of South Africa in December 1976; and provides evidence that adverse weather conditions (heavy seas and gales) can have a negative impact on pup survival at Black Rocks seal colony, Algoa Bay. The report supplements a paper compiled for the World Wide Fund for Nature, ZA348 - part 10(a): Stewardson, C. L., 1999. Impact of the fur seal industry on the distribution and abundance of Cape fur seals, *Arctocephalus pusillus pusillus*, on the Eastern Cape coast of South Africa. *Transactions of the Royal Society of South Africa* 54(2): 217–245. Photographs presented in this study have been donated to the Cape Archives Repository, Roeland Street, Cape Town, South Africa (general photographic collection under references AG17747–AG17760).

Key words: South African (Cape) fur seal, Arctocephalus pusillus pusillus, seal pup mortality, storms, South African Airforce (SAAF), wildlife rescue, Algoa Bay

The Cape fur seal, *Arctocephalus pusillus pusillus*, is South Africa's only endemic seal species. Approximately 1.5 to 2 million seals breed at 25 colonies distributed from Black Rocks (Algoa Bay) on the south-east coast of South Africa, to Cape Cross (Namibia) (Butterworth & Wickens, 1990).

Black Rocks (33°50'S, 26°15'E) is the eastern extreme of the Cape fur seal's breeding range. This small island rookery is located *c.* 9 km south of the nearest land (Fig. 10(b).1). Pup counts conducted over the past 23 years indicate that the Black Rocks population has decreased by 84%, i.e., *c.* 4 520 seals in 1974; *c.* 710 seals in 1997 (Shaughnessy, 1987; SFRI, unpubl. data). Several factors have contributed to the decline in seal numbers (Stewardson unpubl. data), including the influence of storms (Stewardson, 1999; present study).

Female Cape fur seals give birth to one pup every year between November and early December. At Black Rocks, the main breeding rock (the largest rocky outcrop) is the only one capable of supporting pups during heavy seas; the seals can only occupy *c.* 8 360 m^2 (Rand, 1972). When seal numbers increase on this small island, individuals are forced to less sheltered areas. If adverse weather conditions (heavy seas and gales) come early in the pupping season, when pups are unable to swim proficiently, animals inhabiting the less sheltered areas are likely to be washed from the rocks. Although low lying areas are more prone to surging swells, large swells may also break over the main breeding rock which is 6 m above mean sea level (Stewardson, 1999).

Gale force winds and/or large swell waves (≥ 4 m) during the pupping season were responsible for mass strandings (i.e., 50 to 300 pups) at Black Rocks seal colony in December 1974, December 1976, December 1977, January 1986 and December 1987. Three of these mass strandings occurred during warm phase *El Niño* years, i.e., 1976, 1986 and 1987 (Stewardson, 1999). The mass stranding of 1976 is documented below.

December 4–5, 1976

Two yachtsmen, Mr Dave Wentzel and Mr Marc Pudifin, were washed from their Durban based vessel *Cloud Nine* on Saturday December 4, 1976 at the height of a violent east coast storm. Helicopters of 16 squadron, Port Elizabeth, were deployed to search for the missing men (Anonymous, 1976).

On the homeward leg of their rescue mission, air crew sighted numerous Cape fur seal pups stranded along the coastline between East London (32°58'S, 27°58'E) and Woody Cape (33°46'S, 26°19'E) (Fig. 10(b).1). High seas and swell had washed these pups off Black Rocks and carried them to the mainland. Strong south-south westerly winds of 69 kts (max. gust) were recorded at the Port Elizabeth weather station on Saturday, December 4 (G. Samson, pers. comm.). Swell height of 9 m (west-south west) and sea height of 5 m were recorded in the general vicinity on Sunday, December 5 (M. Grundlingh, pers. comm.). The pups were 1–2 weeks of age. Without milk, the pups would soon die.

Dr John Wallace, the director of the Port Elizabeth Museum, approached the South African Airforce (SAAF), requesting that the Port Elizabeth squadron assist with the mass stranding. Wallace requested that the surviving pups be located, and returned to Black Rocks by helicopter. After negotiating with headquarters in Pretoria, Major G. A. Haasbroek (acting officer commanding the Port Elizabeth Airforce Station) agreed to assist with rescue operations.

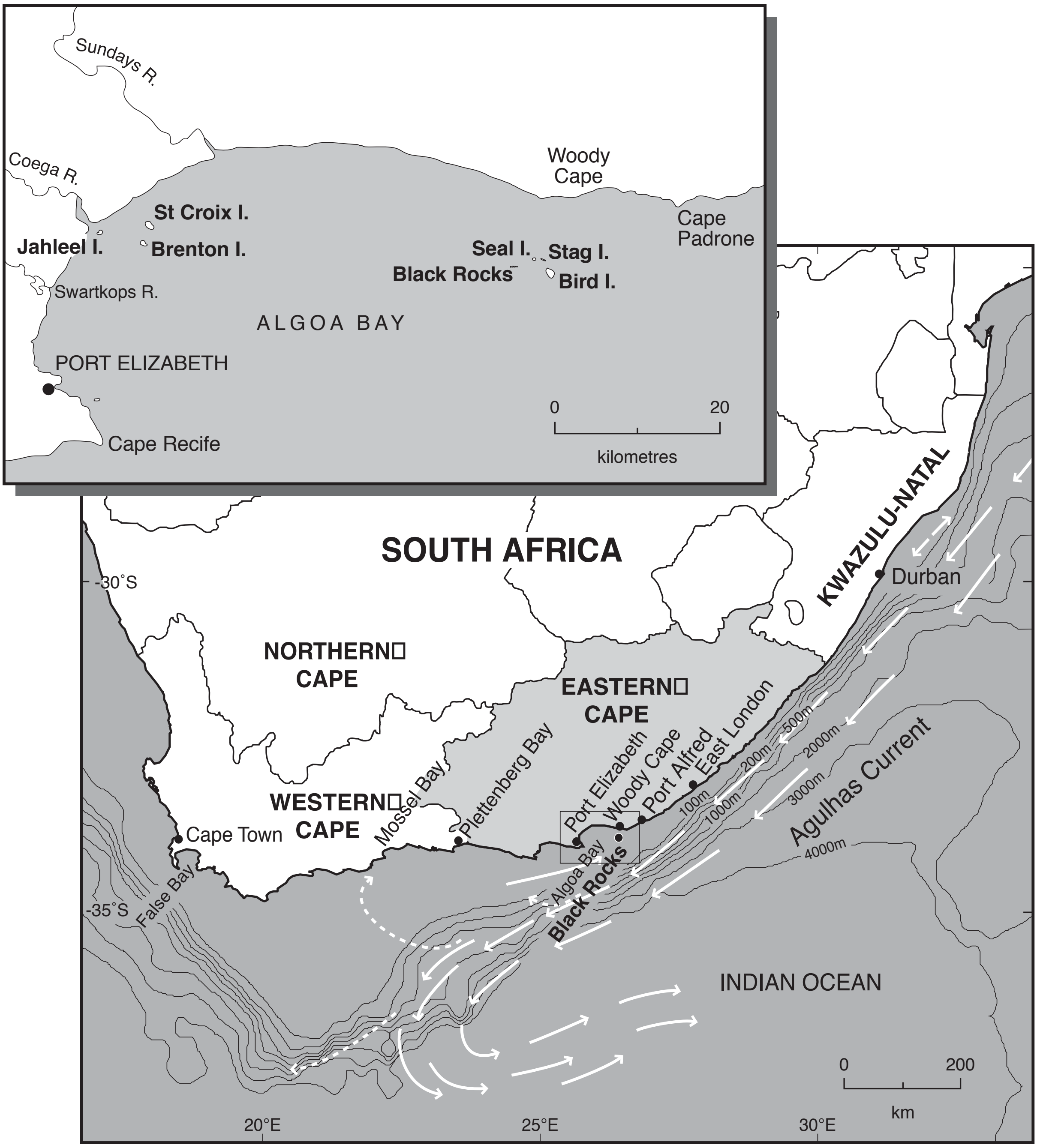

Fig. 10(b).1 Eastern Cape coast of South Africa indicating the position of Black Rocks seal colony, Algoa Bay, and the coastline where the seal pups were stranded, i.e., between Woody Cape and East London.

Figs. 10(b).2–6

Date: Wednesday, December 8, 1976.
Subject: Six stranded seal pups that had been rehabilitated at Port Elizabeth Oceanarium, were taken to the Port Elizabeth Airforce Station and then airlifted to Black Rocks.

Fig. 10(b).2 SAAF flight crew prepare to airlift seal pups from the Port Elizabeth Airforce Station.
The crew had built boxes to secure the seal pups which they placed in the back the helicopter (Alouette III).

Fig. 10(b).3 Seal pups relax before being placed into the helicopter.

Fig. 10(b).4 Seal pup held over the water prior to release at Black Rocks.

Fig. 10(b).5 Pups gently dropped from the hovering helicopter about 20 m from Black Rocks.

Fig. 10(b).6 Pups gently dropped from the hovering helicopter about 20 m from Black Rocks. Numerous seals remain on the rocks indicating minimal disturbance from the helicopters.

December 7–8, 1976

Two Alouette helicopters were deployed for the rescue mission. Three pilots (Lt. Theo Meyer, Lt. Eddie Brown and Lt. Chris Millbank), flight engineers and oceanarium officials searched the coastline from Port Elizabeth to East London over a two day period. The crew counted stranded seal pups and collected survivors.

A total of 80 live pups were located. These pups were airlifted to the Bird Islands and dropped about 20 m from Black Rocks.

The reaction of the seals at Black Rocks to the approaching helicopters was initially one of panic. However, this gradually lessened after the first group of seals left the rocks (G. Ross, pers. comm.).

Twenty one of the 80 pups were tagged (double tagged) by Dr J. H. Wallace and S. Rutherford before release (Appendix 10(b).1). The pups were generally calm and easy to handle.

Figs. 10(b).7–13
Date: Wednesday, December 8, 1976.
Subject: Stranded seal pups retrieved form coastline between Woody Cape and East London by SAAF helicopters.

Fig. 10(b).7 Winch hoist down: crewman lowered from helicopter (Alouette III) at Woody Cape.
The terrain in this area is inaccessible by four wheel drive.

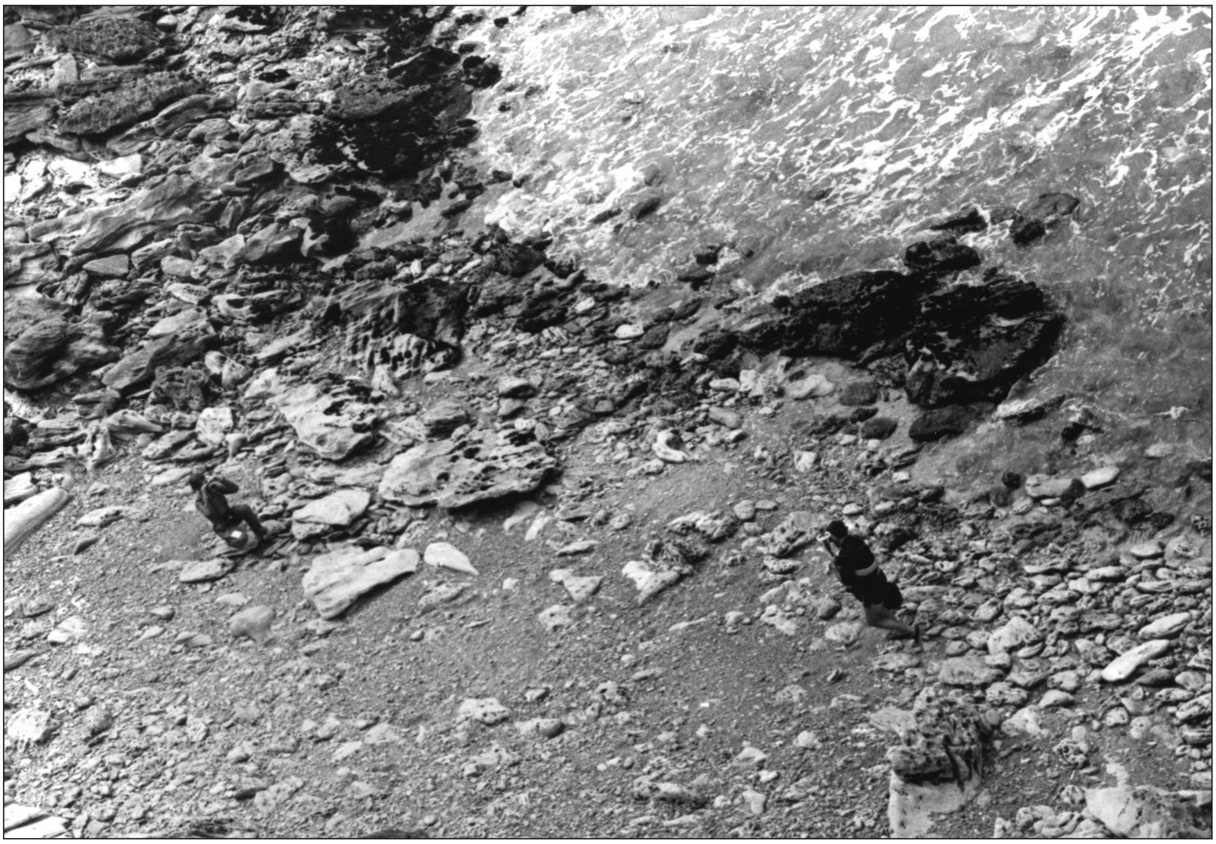

Fig. 10(b).8 Crewman on the ground still attached to hoist cable.

Fig. 10(b).9 Seal pup retrieved by crewman.

Fig. 10(b).10 Helicopter hovers while waiting for crewman to return with stranded seal pup.

Fig. 10(b).11 Winch hoist up: crewman and pup winched to safety.

Fig. 10(b).12 Helicopter puts down on sandy beach to retrieve stranded seal pup.

Fig. 10(b).13 Twenty one seal pups were double tagged before being released at Black Rocks.

December 14, 1976

Six days after the aerial pup count and rescue, an additional 20 pups were recovered from local beaches. Seven of these animals were retained by the Port Elizabeth Oceanarium. Thirteen were tagged (single tag in left flipper) and airlifted to Black Rocks (Appendix 10(b).1). Very few pups were seen on the island (G. Ross, pers. comm.).

Although a total of 100 stranded pups had been recovered since the storm, overall pup mortality was considerably greater. Many pups would have drowned or have been eaten by sharks. A percentage of those that made it ashore may have been slaughtered by beachcombers for food and/or their skins. Many of the pups would have been missed by observers, i.e., pups continued to haul-out on beaches after aerial counts had been conducted.

Figs. 10(b).14–15

Date: December 14, 1976.
Subject: Thirteen pups which had been rehabilitated at the Port Elizabeth Oceanarium were taken to the beach front (Humewood) to be airlifted to Black Rocks. All pups were tagged in the left flipper prior to release.

Fig. 10(b).14 Seal pups placed in Alouette III to be airlifted to Black Rocks.

Fig. 10(b).15 Pups gently dropped from the hovering helicopter about 20 m from Black Rocks.

December 22, 1976

It is not known how many of the orphaned pups were reunited with their mothers. At least two tagged seal pups which had been returned to Black Rocks on December 8 (A2255, A2256 and A2261, A2262) washed up again on the mainland, i.e., stranded at Port Alfred. One of these pups (A2255, A2256) was very weak and died soon after capture (G. Ross, pers. comm.).

January 4, 1977

By January 4, 12 orphaned seal pups were based at the Port Elizabeth Oceanarium. The pups were fed a mixture of cod liver oil, sunflower seed oil, pilchards, glucose and vitamins (Appendix 10(b).2).

February 11, 1977

Oceanarium staff informed the public that new homes must be found for the 12 orphaned pups which had not been returned to Black Rocks. The estimated coast of raising a single pup was R300; each pup had to be fed for at least seven months. Provisional plans were made to give seven of the pups to English firms. The Port Elizabeth Oceanarium kept the remaining five pups (Anonymous, 1977).

Today, when mass seal pup strandings occur off the Eastern Cape coast, Port Elizabeth Oceanarium officials euthanase the stranded animals to prevent unnecessary suffering. For example, more than 200 stranded seals pups were put down in January 1988 (Anonymous, 1988).

We wish to thank Dr V. Cockcroft (Port Elizabeth Museum), Dr J. Hanks (WWF-South Africa) and Prof. A. Cockburn (Australian National University) for financial and logistic support. We express our sincere appreciation to Col. J. Malan and Brig. Gen W. Lord (South African Airforce) for confirming details of the rescue mission. We thank Mr N. Minch (Australian National University) for map design, Dr R. Barwick for photographic manipulation (Australian National University) and Dr G. Ross (Australian Biological Resources Studies, Canberra) for reviewing the manuscript. Photographs were taken by Mr E. Pike. This manuscript is part of a larger study on behalf of the World Wild Fund For Nature – South Africa (Project ZA-348, part 10(b)).

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Appendix 10(b).1 ***Identification numbers: 34 of the 93 stranded seal pups that were returned to Black Rocks were tagged before release***

Tag in both left and right fore-flipper	Tag in left fore-flipper only
1. A2276; A2277	22. A2290
2. A2278; A2279	23. A2275
3. A2280; A2281	24. A2229
4. A2282; A2283	25. A2230
5. A2284; A2285	26. A2231
6. A2286; A2287	27. A2232
7. A2288; A2289	28. A2233
8. A2291; A2292	29. A2234
9. A2293; A2294	30. A2235
10. A2251; A2252	31. A2236
11. A2253; A2254	32. A2237
12. A2255; A2256	33. A2238
13. A2257; A2258	34. A2239
14. A2259; A2260	
15. A2261; A2262	
16. A2263; A2264	
17. A2265; A2266	
18. A2267; A2268	
19. A2269; A2270	
20. A2271; A2272	
21. A2273; A2274	

Appendix 10(b).2 ***Food formula for orphaned Cape fur seal pups***

To 1 pint of warm water add:

2 heaped teaspoons lecithin
2 multivitamin tablets
1 calsuba tablets
2 teaspoons cod liver oil
1 teaspoon glycerin
240 ml sunflower seed oil
2 ml glucose
1 teaspoon salt (NaCl)

Place ingredients in a blender and mix for 2–3 minutes.

Add 4 pilchards and mix at high speed for at least 5 minutes. Pour mixture through a strainer into a bucket.

Then place 1 pint of warm water and 4 pilchards into the blender, mix thoroughly and pour through a strainer. Add this mixture to the mixture already in the bucket.

This formula is sufficient to feed two seal pups per day. Each pup is given 350 ml of formula twice daily.

This formula was used by Port Elizabeth Oceanarium staff to feed orphaned Cape fur seal pups in 1976 and 1977 (Ross, pers. comm.); (1 litre = 1.76 pints).

CHAPTER 11(a)

Operational interactions between Cape fur seals *Arctocephalus pusillus pusillus* and fisheries off the Eastern Cape coast of South Africa: part one, trawl fishing

INTRODUCTION

The “inshore” fishing area off the south and east coasts of South Africa extends from Cape Agulhas (20° E) in the west, to the Great Fish River (27°10’ E) in the east, and seawards to the 110 m depth contour. The main commercial fisheries based in this region are inshore bottom trawling, squid jigging, handline fishing, and hake-directed longline (experimental fishery commenced in 1994). The hake-directed inshore trawl vessels operate up to 70 km from the coast in depths of 50–150 m. The area seawards of the 110 m depth contour is utilised by deep sea trawlers which are restricted from fishing shallower, or inside, the 110 m isobath-contour east of Cape Agulhas 20° E (Peter Sims, pers. comm.).

Off the Eastern Cape coast (Plettenberg Bay, 33° 07’S, 23°25’E, to the Kwazulu-Natal boarder, 31°05’S, 30°11’E), trawling involves dragging a net along the sea bed (bottom trawling) for 2–4 hrs, and then hauling the net to the surface with its catch. The smaller inshore trawlers (14 m to 30 m in length) mainly target hake and sole, at depths of 50–150 m. The larger offshore vessels (30 m to 90 m in length) mainly target hake, at depths of 150–700 m. Inshore and offshore hake-directed trawlers operate from sunrise to sunset, while sole-directed trawlers operate day and night (Peter Sims, pers. comm.).

From 1992 to 1995, the inshore trawl fleet consisted of *c.* 37 vessels (30 based at Mossel Bay and 7 at Port Elizabeth) of which *c.* 10 operated off the Eastern Cape. The sole-directed vessels (*c.* 20) all worked west of Mossel Bay in depths of 50–80 m. The South African deep sea trawl fleet consisted of *c.* 60 vessels (mostly based at Cape Town and Saldanha Bay) which operated off the south/east and west coasts. Apart from the 3 deep sea vessels based at Port Elizabeth, and *c.* 3 small deep-sea vessels from Cape Town (which work grids 518–520), the deep sea fleet operates on the “chalk line” grounds which follow the 200/300 m depth contour. The main component of the deep sea fleet operates off the Cape and off the west coast (Peter Sims, pers. comm.).

The main trawl species off the east coast are shallow water hake (*Merluccius capensis*), deep water hake (*M. paradoxus*), horse mackerel (*Trachurus trachurus capensis*) and Agulhas sole[1] (*Austroglossus pectoralis*). The main by-catch species include kingklip (*Genypterus capensis*), John dory (*Zeus faber*), monk fish (*Lophius* sp.), ribbon fish (*Lepidopus caudatus*), rat tails (*Caelorinchus simorhynchus, C. braueri, Malacocephalus laevis* or *Lucigadus ori*), jacopever (*Helicolenus dactylopterus*), rays (*Raja* spp.), reds (capenter, *Argyrozona argyrozona*; santer, *Cheimerius nufa*r; panga *Pterogymnus laniarius*); and chub mackerel, *Scomber japonicus*.

In 1994, the hake Total Allowable Catch was 148 000 tons, which was divided on a 2:1 basis between the west and south/east coasts. The inshore hake TAC was 9 835 tons for the south/east coast, of which 590 tons was allocated to Port Elizabeth based companies. The deep sea hake TAC was *c.* 2 862 tons for Port Elizabeth based companies. The inshore sole TAC was 872 tons for the south/east coast, of which 35 tons was allocated to Port Elizabeth based companies. The horse mackerel TAC was split into: (i) a sectoral reserve held against bottom trawling deep sea (23 266 tons) and inshore (6 434 tons); and (ii) specific company quotas for directed mid-water (27 894 tons), of which 2 213 tons was held by Port Elizabeth based companies. The estimated landed value of deep sea hake was R2 265 per ton, inshore hake R2 184 per ton, sole R7 000 per ton and horse mackerel R840 per ton (Peter Sims, pers. comm.).

East coast trawl fishermen operate in an area inhabited by Cape fur seals. At the time of this study, *c.* 140 000 Cape fur seals[2] (8.5% of the total population) inhabited the south/east coast, between False Bay and Algoa Bay, at five breeding colonies and one haul-out site (J.H.M. David, pers. comm.). Three of the five colonies (Geyser Rocks, Quoin Rock and Seals Island-False Bay) are situated west of the Agulhas/Atlantic mixing area, i.e., in the south-east Atlantic ocean. The remanding three colonies (Seal Island-Mossel Bay, Rondeklippe-Plettenberg Bay and Black Rocks-Algoa Bay) are situated further east, in the south-west Indian ocean, inshore of the warm Agulhas Current (20°C–25°C) (Rand, 1967). Considering that some of the species eaten by Cape fur seals are of commercial importance to this industry (chapter 9), it is inevitable that seals and fisheries will come into conflict when fishing.

Some trawl fishermen complain that seals: consume large quantities of commercially important fish species which would otherwise be available to the industry; take fish from nets; damage nets and propellers; and disrupt fishing operations (when trapped in the factory area). The extent of the problem is not known.

Seals foraging on commercial trawl grounds are at risk. Seals are incidentally drowned in trawl nets, and deliberately killed (when trapped in the factory area). The effects of this on the local seal population are unknown, but unlike the west coast population, that on the Eastern Cape coast is not increasing.

Research examining operational interactions between seals and the trawl fishing industry has been conducted on the west and south coast of southern Africa (Rand, 1959; Shaughnessy & Payne, 1979; Shaughnessy, 1985; Anon., 1987; Ryan & Moloney, 1988; David 1987; Wickens, 1989; Wickens *et al.,* 1992; Wickens, 1994); however, there is no comprehensive information for the Eastern Cape coast.

[1] Sole is mainly caught south-west of Plettenberg Bay.

[2] Inferred from pup counts for 1993.

This study documents an evaluation of operational interactions between the trawl fishing industry and Cape fur seals, in waters off the Eastern Cape coast of Southern Africa. Information was obtained from independent observation aboard commercial trawl vessels over a 57 day period (*n* = 196 trawls).

METHODS

Information on seal-fisheries operational interactions was collected by direct observation aboard commercial trawl vessels from July 1992 and April 1994. Observations focused on six key areas: (i) fishing operations; (ii) seal attendance; (iii) depredation and scavenging (feeding from nets; feeding on offal and discarded by-catch; (iv) damage to equipment; (v) disruption to fishing operations; and (vi) seal mortality (number of seals entrapped in nets; numbers drowned; numbers brought aboard alive; numbers deliberately killed by crew).

Information on the biology of drowned animals was also collected. Standard necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). Upper canines were collected for age determination.

Age was estimated from counts of growth layer groups in the dentine of thin tooth sections. Reproductive condition of males was determined by histological examination of the gonads (presence/absence of sperm in the epididymis).

Observations of seal-fisheries interactions were conducted from three deep sea commercial vessels–one side trawler (*Zuiderzee*) and two stern trawlers (*Midharvid*[3] and *Maria Clare*):

The *Zuiderzee* (30 m in length) has a fishing capacity of 35 tons. Average catch per year is *c.* 800 tons. The catch is preserved on ice. The usual length of fishing trip is 5–10 days, three times each month. As with all side trawlers, the catch is brought aboard over the side of the vessel.

The *Midharvid* (39 m in length) has a fishing capacity of 150 tons. Average catch per year is *c.* 1 500 tons. Some of the catch is frozen and some packed on ice. The usual length of trip is 4 days, eight times each month. As with all stern trawlers, the catch is brought aboard over the stern ramp of the vessel.

The *Maria Clare* (52 m in length) has a fishing capacity of 270 tons. Average catch per year is *c.* 3 600 tons. The catch is frozen. The usual length of trip is 21 days, once each month.

Preliminary analysis of 'seal attendance counts' found that the number of seals observed while hauling was significantly different for side and stern trawlers, therefore information for the two types of trawlers are presented separately. Means are always followed by the standard error.

RESULTS

Side trawl fishing

Fishing operations

A total of 33 days were spent aboard the *Zuiderzee* during which time 94 trawls were observed (Table 11(a).1).

Table 11(a).1 ***Details of trips to observe seal-fisheries interactions during side trawling operations (independent observer aboard the Zeiderzee, n = 94 trawls)***

Trip No.	Start–End date[1]	No. of days at sea[1]	Total hours at sea[1]	No. of trawls observed	No. of trawls per day[2] (range)	Mean duration of trawl[3] ± SE (range)	Total trawl[3] hours
1	20/7/92–25/7/92	6	144	15	3 (1–3)	3 hrs 45 min ± 9 min (3 hrs–5 hrs)	56 hrs 18 min
2	11/8/92–14/8/92	4	96	13	3 (3–4)	3 hrs 2 min ± 11 min (2 hrs 20 min–4 hrs 50 min)	39 hrs 25 min
3	18/8/92–22/8/92	5	120	16	3 (3–4)	3 hrs 23 min ± 8 min (2 hrs 50 min–4 hrs 25 min)	47 hrs 27 min
4	31/10/92–9/11/92	10	240	29	4 (1–5)	3 hrs 7 min ± 8 min (40 min–3 hrs 50 min)	90 hrs 15 min
5	17/5/93–22/5/93	6	144	17	3 (2–3)	3 hrs 26 min ± 8 min (2 hrs 15 min–4 hrs 45 min)	58 hrs 22 min
6	19/4/94–20/4/94	2	48	4	- (1–3)	2 hrs 50 min ± 19 min (2 hrs 15 min–3 hrs 35 min)	11 hrs 21 min
6		**33**	**792**	**94**	**3 (1–5)**	**3 hrs 18 min ± 4 min**	**303 hr 8 min**

[1] Analysis excludes: (i) time taken to steam to fishing grounds; (ii) time net is aboard the vessel; and (iii) time taken to return to port after the last trawling operation, i.e., active trawl time only.

[2] Mode followed by range in round brackets.

[3] Trawl end times for 2 of the 94 trawls were not recorded, *n* = 92.

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[3] The *Midharvid* is not a true stern trawler although the codend has to be lifted over the stern, onto the deck. A true stern trawler has a ramp to the water level, which then allows the codend to be hauled up the ramp quickly.

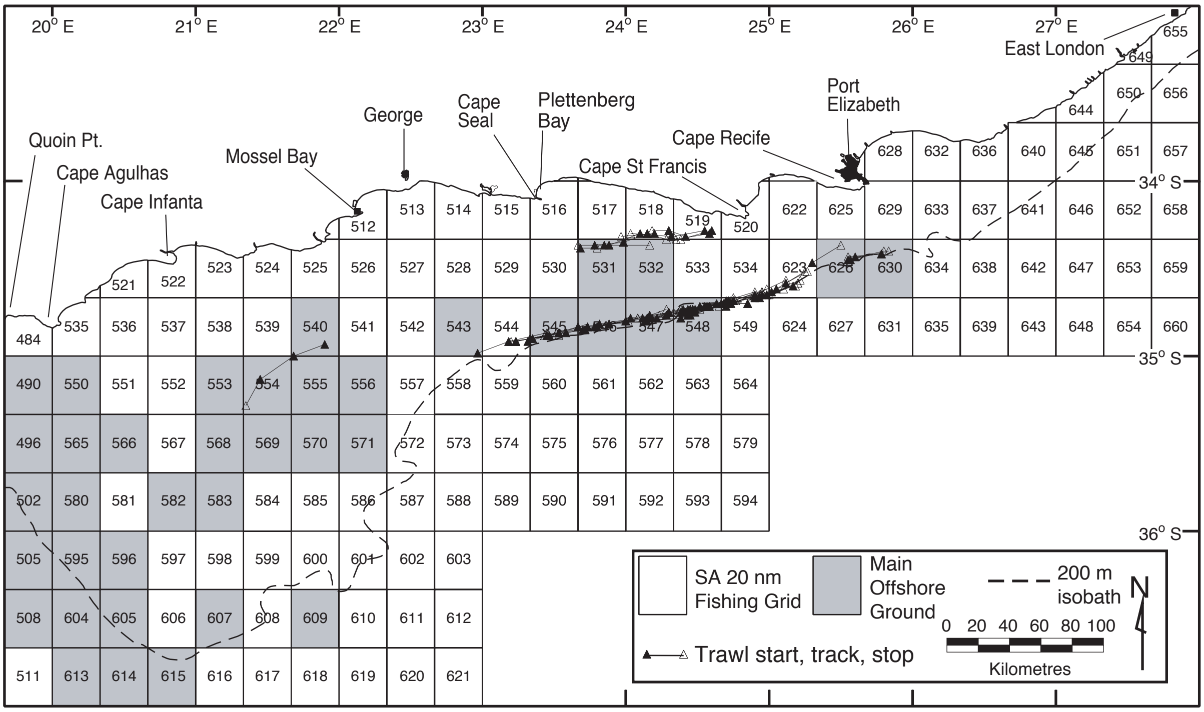

Fig. 11(a).1 Distribution of fishing effort (n = 93 trawls) aboard a commercial side trawler (*Zuiderzee*): start position and end position of individual trawls.
Trawl end position for 1 of the 94 trawls was not recorded, n = 93. Shaded areas represent the main offshore trawl grounds. The demersal grid system is divided into sub-areas (west 1.6, south 2.1 and east 2.2), with the division between east and south occurring at 25° E. The survey area off the Eastern Cape coast overlaps the two sub-areas.

Main target species and corresponding fishing locations

The main target species was hake, with limited catches of horse mackerel. The main by-catch species included John dory, monk fish, rat tails, jacopever and rays. Distribution of fishing effort is presented in fig. 11(a).1.

Minimum distance travelled when trawling

The net was dragged over a minimum distance of 1 064.0 nautical miles (n = 33 days). Mean minimum distance of a single trawl was 11.4 ± 0.3 nautical miles (Table 11(a).2).

Trawl times

The time of day that the *Zuiderzee* was actively fishing ranged from 0515–1945 hrs (n = 92 trawls). Mean start time for the first trawl of the day was 0642 hrs ± 20 min; second trawl was 1000 hrs ± 9 min (n = 28); third trawl was 1353 hrs ± 19 min; and the fourth trawl was 1534 hrs ± 35 min. On one occasion a fifth trawl was conducted (start time: 1530 hrs) (Fig. 11(a).2).

Fishing depth

The net was dragged at depths ranging from 106.1–398.7 m. Mean fishing depth was 237.2 ± 9.1 m; median 221.3 m (Table 11(a).3).

Table 11(a).2 ***Minimum distance travelled in nautical miles when trawling aboard the Zeiderzee (n = 93 trawls, side trawler)***

Trip No.	No. of trawls observed	Mean distance travelled per trawl Mean ± SE	Mean distance travelled per trawl Range	Total trawl distance per trip
1	15	10.97 ± 0.73	4.58–15.13	164.57
2	13	10.06 ± 1.06	5.85–18.36	130.75
3	14[1]	11.97 ± 0.50	8.77–15.14	191.52
4	29	11.05 ± 0.48	5.80–15.14	320.43
5	17	12.77 ± 0.85	8.44–23.13	204.30
6	4	13.10 ± 1.11	10.96–15.73	52.41
6	**921**	**11.44 ± 0.31**	**4.58–23.13**	**1063.98**

[1] Trawl end position for 1 of the 94 trawls was not recorded, n = 93.

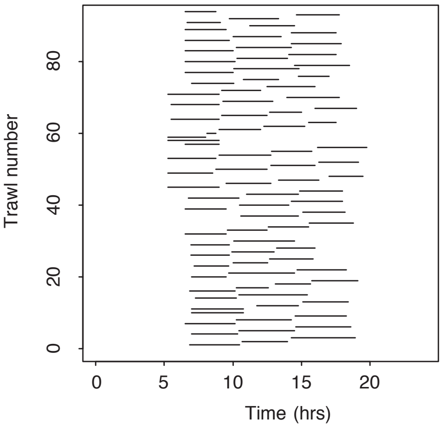

Fig. 11(a).2 Time of day side trawler actively fishing (n = 92 trawls).
Horizontal lines represent total trawl time for individual trawls (start time to end time for 92 trawls).
Trawl end times for 2 of the 94 trawls were not recorded, n = 92.

Table 11(a).3 ***Water depth[1] at which the trawl net was dragged (n = 94 trawls, side trawler)***

Trip No.	No. of trawls observed	Water depth[1] (m) Mean ± SE	Water depth[1] (m) Range
1	15	195.68 ± 2.86	184.71–228.60
2	13	278.50 ± 11.20	226.80–356.60
3	16	271.80 ± 16.90	188.40–371.20
4	29	263.20 ± 23.00	111.60–398.70
5	17	193.00 ± 11.40	106.1–254.20
6	4	118.87 ± 2.69	113.39–124.36
6	**94**	**237.18 ± 9.14**	**106.10–398.70**

[1] Depth is based on trawl start times. However, net depth may be adjusted during the trawl depending on the quantity of fish entering the net, etc.

Seal attendance

Number of seals in the vicinity of nets while hauling

The mean number of seals observed in the vicinity of the net (while the full net was hauled to the water surface and loaded over the side of the vessel) was 10.7 ± 0.8; median 9 (*n* = 92 hauls) (Table 11(a).4). At least one seal was observed near the net during most (98%) hauls, and less than 10 seals were observed at *c*. 50% of the hauls (Table 11(a).5). The maximum number of seals observed during a single haul was 36.

Table 11(a).4 ***Number of seals in the vicinity of net during hauling operations (n = 92 trawls, side trawler)***

Trip No.	No. of trawls	No. of seals[2] Mean ± SE	No. of seals Range
1	15	17.67 ± 2.18 (18)	5–36
2	13	15.85 ± 1.95 (14)	7–34
3	15[1]	10.27 ± 1.54 (10)	4–22
4	29	6.14 ± 1.16 (4)	0–28
5	16[1]	8.69 ± 0.87 (8)	5–18
6	4	11.50 ± 2.50 (11)	6–18
6	**92[1]**	**10.74 ± 0.79 (9.0)**	**0–36**

[1] Counts not conducted during 2 of the 94 trawls, *n* = 92.

[2] Median given in round brackets.

Table 11(a).5 ***Percent frequency of seals in the vicinity of net during hauling operations (n = 92 hauls, side trawler)***

No. of seals	No. of trawls	Percent of hauls	Cumulative percent
0	2	2.2	2.2
1	3	3.3	5.4
2	3	3.3	8.7
3	3	3.3	12.0
4	8	8.7	20.7
5–9	29	31.5	52.2
10–19	33	35.9	88.0
20–29	9	9.8	97.8
30-39	2	2.2	100.0
	92[1]		

[1]Counts not conducted during 2 of the 94 trawls, *n* = 92.

Depredation and scavenging

Number of seals feeding directly from the net

The mean number of seals observed feeding directly from the net (while the full net was hauled to the water surface and loaded over the side of the vessel) was 10.1 ± 0.8; median 8 (*n* = 92 hauls) (Table 11(a).6). At least one seal was observed feeding from the net during most (91%) hauls. Less than 10 seals were observed feeding from the nets at *c*. 50% of the hauls (Table 11(a).7). The maximum number of seals observed feeding from the nets during a single haul was 36.

Table 11(a).6 ***Number of seals feeding directly from the net during hauling operations (n = 92 hauls, side trawler)***

Trip No.	No. of trawls	No. of seals[2] Mean ± SE	No. of seals Range
1	15	17.67 ± 2.18 (18)	5–36
2	13	15.85 ± 1.95 (14)	7–34
3	15[1]	10.27 ± 1.54 (10)	4–22
4	29	5.69 ± 1.21 (4)	0–28
5	16[1]	8.69 ± 0.87 (8)	5–18
6	4	0	0
6	**92[1]**	**10.10 ± 0.83 (8)**	**0–36**

[1] Counts not conducted during 2 of the 94 trawls, *n* = 92.

[2] Median given in round brackets.

Table 11(a).7 ***Percent frequency of seals feeding directly from the net during hauling operations (n = 92 hauls, side trawler)***

No. of seals	No. of trawls	Percent of trawls	Cumulative percent
0	8	8.7	8.7
1	5	5.4	14.1
2	1	1.1	15.2
3	4	4.4	19.6
4	7	7.6	27.2
5–9	26	28.3	55.4
10–19	30	32.6	88.0
20–29	9	9.8	97.8
30-39	2	2.2	100.0
	92[1]		

[1]Counts not conducted during 2 of the 94 trawls, *n* = 92.

Number of seals feeding on offal and discarded by-catch

The mean number of seals feeding on discarded fish head/gut (offal) and whole fish (by-catch) was 10.6 ± 0.8; median 8.5 (*n* = 92) (Table 11(a).8). At least one seal was observed feeding on discarded offal/by-catch during most (97%) hauls, and less than 10 seals were observed feeding on discarded offal/by-catch at *c*. 50% of the hauls (Table 11(a).9). The maximum number of seals observed feeding on discarded offal/by-catch during a single haul was 36.

Table 11(a).8 ***Number of seals feeding on discarded offal/by-catch (n = 92 hauls, side trawler)***

Trip No.	No. of trawls	No. of seals[2] Mean ± SE	No. of seals Range
1	15	17.67 ± 2.18 (18)	5–36
2	13	15.85 ± 1.95 (14)	7–34
3	15[1]	10.27 ± 1.54 (10)	4–22
4	29	6.00 ± 1.18 (4)	0–28
5	16[1]	7.88 ± 0.63 (7.5)	5–15
6	4	11.50 ± 2.50 (11.0)	6–18
6	**92[1]**	**10.55 ± 0.79 (8.5)**	**0–36**

[1] Counts not conducted during 2 of the 94 trawls, *n* = 92.

[2] Median given in round brackets.

Table 11(a).9 ***Percent frequency of seals feeding on discarded offal/by-catch (n = 92 hauls, side trawler)***

No. of seals	No. of trawls	Percent of trawls	Cumulative percent
0	3	3.3	3.3
1	3	3.3	6.5
2	3	3.3	9.8
3	3	3.3	13.0
4	7	7.6	20.7
5–9	30	32.6	53.3
10–19	32	34.8	88.0
20–29	9	9.8	97.8
30-39	2	2.2	100.0
	92[1]		

[1] Counts not conducted during 2 of the 94 trawls, *n* = 92.

Damage to equipment

Although seals did not tear/damage nets directly, on one occasion, two entrapped seals were cut from the net and released alive. Therefore the incidence of net damage was 1.06 per 100 trawls (based on 94 trawls).

On July 22, 1992 two entrapped seals were cut from the net and released alive. The cut measured *c.* 50 cm × 50 cm and took 5–10 min to repair. At the time, a large number of seals were in the area, i.e., 36 seals were observed in the vicinity of the net while hauling.

No propeller damage was reported during this study.

Disturbance to operations

Apart from cutting two seals from the net, seals did not cause disruption to fishing operations. Live seals that were brought aboard the vessel returned to sea immediately, i.e., no animals were trapped in the factory area.

Seal mortality or injury

Number of seals incidentally entrapped in the net

A total of 28 seals were incidentally entrapped in nets during the 92 trawls (Table 11(a).10). The mean number of seals entrapped in nets was 30.4 ± 6.7 per 100 trawls. The maximum number of seals entrapped during a single trawl was three.

11(a).10 ***Number of seals incidentally entrapped in the net (n = 92 trawls, side trawler)***

Trip No.	No. of trawls	No. seals caught per trawl 0	1	2	3
1	15	7	5	3	0
2	13	9	2	2	0
3	15[1]	12	2	1	0
4	29	28	1	0	0
5	16[1]	12	3	0	1
6	4	4	0	0	0
6	**92[1]**	**72**	**13**	**6**	**1**

[1] Counts not conducted during 2 of the 94 trawls, *n* = 92.

Number of seals incidentally entrapped in the net and returned to sea alive

Of the 28 seals incidentally entrapped in nets, 12 (43%) were returned to sea alive (Table 11(a).11). The mean number of seals that returned to sea alive was 13.0 ± 3.9 per 100 trawls. The maximum number of seals retuned to sea alive in a single trawl was two.

Table 11(a).11 ***Number of seals incidentally entrapped in the net and returned to sea alive (n = 92 trawls, side trawler)***

Trip No.	No. of trawls	No. seals caught per trawl 0	1	2
1	15	11	3	1
2	13	11	2	0
3	15[1]	13	2	0
4	29	29	0	0
5	16[1]	13	3	0
6	4	4	0	0
6	**92[1]**	**81**	**10**	**1**

[1] Counts not conducted during 2 of the 94 trawls, *n* = 92.

Number of seals that incidentally drowned in the net

Of the 28 seals incidentally entrapped in nets, 16 (57%) had drowned (Table 11(a).12). The mean number of seals incidentally drown was 17.4 ± 4.5 per 100 trawls. The maximum number of seals that had drowned in a single trawl was two.

Table 11(a).12 ***Number of seals incidentally drowned in the net (n = 92 trawls, side trawler)***

Trip No.	No. of trawls	No. seals incidentally drowned per trawl 0	1	2
1	15	10	4	1
2	13	9	4	0
3	15[1]	13	2	0
4	29	28	1	0
5	16[1]	14	1	1
6	4	4	0	0
6	**92[1]**	**78**	**12**	**2**

[1] Counts not conducted during 2 of the 94 trawls, *n* = 92.

Table 11(a).13 ***Details of trips to observe seal-fisheries interactions during stern trawling operations (independent observer aboard the Maria Clare and the Midharvid, n = 102 trawls)***

Trip No.	**Start-End date**[1]	**No. of days at sea**[1]	**Total hours at sea**[1]	**No. of trawls observed**	**No. of trawls per day**[2] **(range)**	**Mean duration of trawl**[3] **± SE (range)**	**Total trawl**[3] **hours**
1	7/9/92–25/9/92	19	456	71	4 (1–5)	3 hrs 22 min ± 6 min (1 hr 20 min–6 hrs 15 min)	215 hrs 56 min
2	23/6/93–27/6/93	5	120	31	4 (2–4)	2 hrs 22 min ± 6 min (1 hr 30 min–3 hrs 35 min)	73 hrs 21 min
2		**24**	**576**	**102**	**4 (1–5)**	**3 hrs 22 min ± 6 min** **(1 hr 20 min–6 hrs 15 min)**	**289 hrs 17 min**

[1] Analysis excludes: (i) time taken to steam to fishing grounds; (ii) time net is aboard the vessel; and (iii) time taken to return to port after the last trawling operation, i.e., active trawl time only.

[2] Mode followed by range in round brackets.

[3] Trawl start times for 2 of the 102 trawls, and trawl end times for 7 of the 102 trawls, were not recorded, *n* = 95.

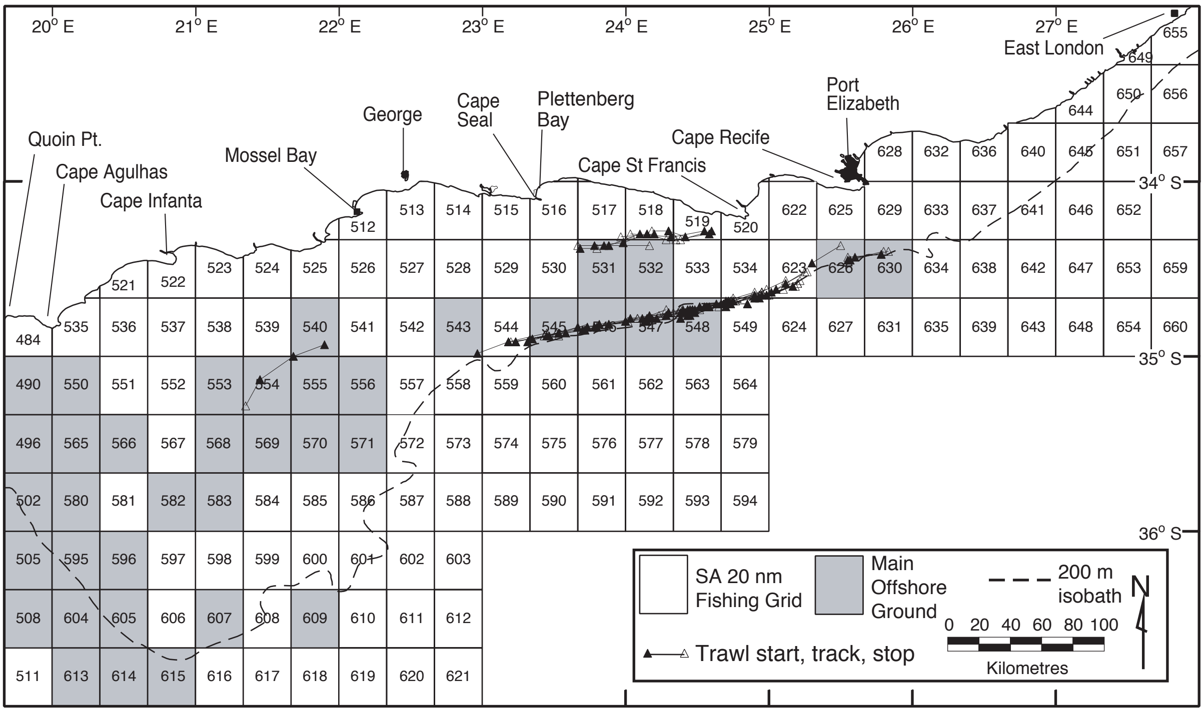

Fig.11(a).3 Distribution of fishing effort (*n* = 100 trawls) aboard a commercial stern trawler (*Maria Clare; Midharvid*): start position and end position of individual trawls.
Trawl end position for 2 of the 102 trawls was not recorded, *n* = 100. Shaded areas represent the main offshore trawl grounds. The demersal grid system is divided into sub-areas (west 1.6, south 2.1 and east 2.2), with the division between east and south occurring at 25° E. The survey area off the Eastern Cape coast overlaps the two sub-areas.

Number of seals deliberately killed by the captain/crew

No seals were killed by the captain or crew. All seals that came aboard alive (*n* = 12) in the net were allowed to return to sea unharmed, i.e., individual animals jumped over the side or the stern of the vessel. All seals returned to the water immediately.

Stern trawl fishing

Fishing operations

A total of 24 days were spent aboard the *Midharvid* and *Maria Clare* during which time 102 trawls were observed (Table 11(a).13).

Main target species and corresponding fishing locations

The main target species was hake, with limited catches of horse mackerel. The main by-catch species included ribbon fish, John dory, monk fish, rat tails, jacopever and rays. Distribution of fishing effort is presented in fig. 11(a).3.

Minimum distance travelled when trawling

The nets of the two trawlers were dragged over a combined minimum distance of 1 132.1 nautical miles. Mean minimum distance of a single trawl was 11.4 ± 0.5 nautical miles (Table 11(a).14).

Trawl times

Table 11(a).14 ***Minimum distance travelled in nautical miles when trawling (n = 100 trawls, stern trawlers)***

Trip No.	No. of trawls observed	Mean distance traveled per trawl Mean ± SE	Mean distance traveled per trawl Range	Total trawl distance per trip
1	69[1]	12.03 ± 0.62	2.47–38.07	818.41
2	31	10.11 ± 0.77	5.07–26.98	313.67
2	**100[1]**	**11.44 ± 0.49**	**2.47–38.07**	**1132.08**

[1] Trawl end position for 2 of the 102 trawls was not recorded, $n = 100$.

The time of day that the stern trawlers were actively fishing ranged from 0107–2600 hrs, i.e., on one occasion the first trawl of the day started early in the morning at 0107 hrs; and several trawls which stated late at night ended near midnight, or early the following morning at 0030 hrs and 0200 hrs ($n = 95$ trawls).

Mean start time for the first trawl of the day was 0623 hrs ± 27 min; second trawl was 0958 hrs ± 17 min; third trawl was 1320 hrs ± 19 min; and the fourth trawl was 1550 hrs ± 23 min. On one occasion a fifth trawl was conducted (start time: 2115 hrs) (Fig. 11(a).4).

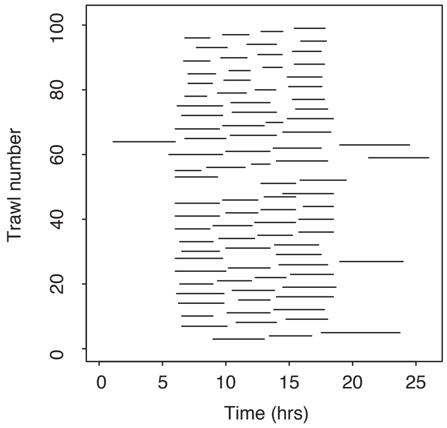

Fig. 11(a).4 Time of day stern trawler actively fishing ($n = 95$ trawls).
Horizontal lines represent total trawl time for individual trawls (start time to end time for 95 trawls; 1–5 trawls per day over 24 days).
Trawl start times for two of the 102 trawls and trawl end times for seven of the 102 trawls, were not recorded, $n = 95$.

Fishing depth

The nets were dragged at depths ranging from 125.0–331.0 m. Mean fishing depth was 203.3 ± 5.5 m; median 186.1 m (Table 11(a).15).

Table 11(a).15 ***Water depth[1] at which the trawl nets were dragged (n = 100 trawls, stern trawlers)***

Trip No.	No. of trawls observed	Water depth[1] (m) Mean ± SE	Water depth[1] (m) Range
1	69[2]	187.95 ± 6.22	124.96–309.17
2	31	237.48 ± 48.10	138.00–331.00
2	**100[2]**	**203.30 ± 5.53**	**124.96–331.00**

[1] Depth is based on trawl start times. However, net depth may be adjusted during the trawl depending on the quantity of fish entering the net, etc.

[2] Depth for 2 of the 102 trawls was not recorded, $n = 100$.

Seal attendance

Number of seals in the vicinity of nets while hauling

The mean number of seals observed in the vicinity of the net (while the full net was hauled to the water surface and brought aboard over the stern of the vessel) was 6.3 ± 0.7; median 4 ($n = 95$ hauls) (Table 11(a).16). At least one seal was observed near the net during most (87%) hauls, and ≤ 4 seals were observed at *c.* 50% of the hauls (Table 11(a).17). The maximum number of seals observed during a single haul was 37.

Table 11(a).16 ***Number of seals in the vicinity of net during hauling operations (n = 98 trawls, stern trawlers)***

Trip No.	No. of trawls	No. of seals[2] Mean ± SE	No. of seals Range
1	67[1]	4.18 ± 0.54 (3)	0–18
2	31	10.94 ± 1.45 (8)	0–37
2	**98[1]**	**6.32 ± 0.67 (4.0)**	**0–37**

[1] Counts not conducted during 4 of the 102 trawls, $n = 98$ trawls.

2 Median given in round brackets.

Table 11(a).17 ***Percent frequency of seals in the vicinity of net during hauling operations (n = 98 hauls, stern trawlers)***

No. of seals	No. of trawls	Percent of hauls	Cumulative percent
0	13	13.27	13.27
1	4	4.08	17.35
2	13	13.27	30.61
3	15	15.31	45.92
4	6	6.12	52.04
5–9	25	25.51	77.55
10–19	19	19.39	96.94
20–29	1	1.02	97.96
30-39	2	2.04	100.00
	98[1]		

[1] Counts not conducted during 4 of the 102 trawls, $n = 98$.

Depredation and scavenging

Number of seals feeding directly from the net

The mean number of seals observed feeding directly from the net (while the full net was hauled to the water surface and brought aboard over the stern of the vessel) was 6.3 ± 0.7; median 4 (*n* = 95 hauls) (Table 11(a).18). At least one seal was observed feeding from the net during most (85%) hauls, and ≤ 4 seals were observed at *c.* 50% of the hauls (Table 11(a).19). The maximum number of seals observed feeding from the nets during a single haul was 37.

Table 11(a).18 ***Number of seals feeding directly from the net during hauling operations (n = 95 hauls, stern trawlers)***

Trip No.	No. of trawls	No. of seals[2] Mean ± SE	No. of seals Range
1	64[1]	4.08 ± 0.54 (3)	0–18
2	31	10.87 ± 1.46 (8)	0–37
2	**95**[1]	**6.30 ± 0.68 (4)**	**0–37**

[1] Counts not conducted during 7 of the 102 trawls, *n* = 95.

[2] Median given in round brackets.

Table 11(a).19 ***Percent frequency of seals feeding directly from the net during hauling operations (n = 95 hauls, stern trawlers)***

No. of seals	No. of trawls	Percent of trawls	Cumulative percent
0	14	14.74	14.74
1	4	4.21	18.95
2	11	11.58	30.53
3	14	14.74	45.26
4	6	6.32	51.58
5–9	25	26.32	77.89
10–19	18	18.95	96.84
20–29	1	1.05	97.89
30-39	2	2.11	100.00
	95[1]		

[1] Counts not conducted during 7 of the 102 trawls, *n* = 95.

Number of seals feeding on offal and discarded by-catch

The mean number of seals feeding on discarded fish head/gut (offal) and whole fish (by-catch) was 6.3 ± 0.7; median 4 (*n* = 95 hauls) (Table 11(a).20). At least one seal was observed feeding on discarded offal/by-catch during most (85%) hauls, and ≤ 4 seals were observed feeding on discarded offal/by-catch at *c.* 50% of the hauls (Table 11(a).21). The maximum number of seals observed feeding on discarded offal/by-catch during a single haul was 37.

Damage to equipment

No net damage, or propeller damage, attributed to seal activity was observed in this study.

Table 11(a).20 ***Number of seals feeding on discarded offal/by-catch (n = 94 hauls, stern trawlers)***

Trip No.	No. of trawls	No. of seals[2] Mean ± SE	No. of seals Range
1	63[1]	4.11 ± 0.55 (3)	0–18
2	31	10.87 ± 1.46 (8)	0–37
2	**94**[1]	**6.34 ± 0.69 (4)**	**0–37**

[1] Counts not conducted during 8 of the 102 trawls, *n* = 94.

2 Median given in round brackets.

Table 11(a).21 ***Percent frequency of seals feeding on discarded offal/by-catch (n = 94 hauls, stern trawlers)***

No. of seals	No. of trawls	Percent of trawls	Cumulative percent
0	14	14.89	14.89
1	4	4.26	19.15
2	10	10.64	29.79
3	14	14.89	44.68
4	6	6.38	51.06
5–9	25	26.60	77.66
10–19	18	19.15	96.81
20–29	1	1.06	97.87
30-39	2	2.13	100.00
	94[1]		

[1] Counts not conducted during 8 of the 102 trawls, *n* = 94.

Disturbance to operations

One seal brought aboard the vessel was trapped in the factory area. Fish processing stopped for *c.* 10 minutes, after which time the seal was killed.

Seal mortality or injury

Number of seals incidentally entrapped in the net

A total of 21 seals were incidentally entrapped in nets during the 98 trawls (Table 11(a).22). The mean number of seals entrapped in nets was 21.4 ± 8.5 per 100 trawls. The maximum number of seals entrapped during a single trawl was seven.

Table 11(a).22 ***Number of seals incidentally entrapped in the net (n = 98 trawls, stern trawlers)***

Trip No.	No. of trawls	No. seals caught per trawl 0	1	2	3	7
1	67[1]	62	4	0	1	0
2	31	25	3	2	0	1
2	**98**[1]	**87**	**7**	**2**	**1**	**1**

[1] Counts not conducted during 4 of the 102 trawls, *n* = 98.

Number of seals incidentally entrapped in the net and returned to sea alive

Of the 21 seals incidentally entrapped in nets, 10 (48%) were returned to sea alive (Table 11(a).23). The mean number of seals that returned to sea alive was 10.2 ± 5.5 per 100 trawls. The maximum number of seals returned to sea alive in a single trawl was five.

Table 11(a).23 *Number of seals incidentally entrapped in the net and returned to sea alive (n = 98 trawls, stern trawlers)*

Trip No.	No. of trawls	No. seals caught per trawl 0	1	5
1	67[1]	65	2	0
2	31	27	3	1
2	**98**[1]	**92**	**5**	**1**

[1] Counts not conducted during 4 of the 102 trawls, *n* = 98.

Number of seals that incidentally drowned in the net

Of the 21 seals incidentally entrapped in nets, 10 (48%) had drowned (Table 11(a).24). The mean number of seals incidentally drown was 10.2 ± 3.7 per 100 trawls. The maximum number of seals that had drowned in a single trawl was two.

Table 11(a).24 *Number of seals incidentally drowned in the net (n = 98 trawls, stern trawlers)*

Trip No.	No. of trawls	No. seals incidentally drowned per trawl 0	1	2
1	67[1]	63	4	0
2	31	27	2	2
2	**98**[1]	**90**	**6**	**2**

[1] Counts not conducted during 4 of the 102 trawls, *n* = 98.

Number of seals deliberately killed by the captain/crew

Of the ten seals that came aboard alive, entrapped in the net, one was deliberately killed by the crew, i.e., 1.02 seals per 100 trawls (based on 98 trawls).

On September 24, 1992 an adult male seal was trapped in the factory area. The animal was subsequently killed to prevent possible harm to crew. The animal was hit on the head with a spade, hauled to the deck with ropes, and thrown overboard.

DISCUSSION

In waters off the Eastern Cape coast interactions between the trawl fishing industry and Cape fur seals can result in: (i) revenue losses to fishermen and (ii) mortality/injury to seals.

Seal attendance

On the Eastern Cape coast, at least one seal was observed near the net during most hauls. The mean number of seals observed in the vicinity of commercial trawl vessels (when the net was hauled aboard) was 11 for side trawlers and 6 for stern trawlers. Seal attendance figures were significantly higher for side trawlers (T = 4.29, p = 0.000, df = 180) (present study).

Counts of Cape fur seals from commercial trawl vessels for the south coast are: 4 (Shaughnessy & Payne, 1979), 3 (offshore trawlers) (Wickens, 1994) and 10 (inshore trawlers) (Wickens, 1994). Counts for the west coast are: 6 (Shaughnessy & Payne, 1979) and 18 (offshore trawlers) (Wickens, 1994). Thus, mean attendance estimates for the Eastern Cape coast are comparatively high (present study).

Seal attendance figures are higher on the west coast than in other areas because there are larger seal colonies on the west coast, and offshore trawling takes places closer inshore and is therefore more accessible to seals (Wickens, 1994).

Seal attendance figures on the Eastern Cape coast (present study) were higher than on the south coast. Regional differences may be partially attributed to two factors: (i) the type of vessel, and (ii) the number of vessels in the vicinity when hauling. On the south coast, Wickens (1994) conducted all counts from stern trawlers, and other vessels were visible on 40% of observed hauls. In comparison, on the Eastern Cape coast (present study) half of the counts were made from side trawlers (more seals attend side trawl operations), and other vessels were visible on 3% of the observed hauls (seals not distributed between vessels).

Depredation and damage to equipment

Number of seals feeding directly from the net

On the Eastern Cape coast, at least one seal was observed feeding directly from the net during most hauls. The mean number of seals observed feeding directly from the net was 10 for side trawlers, and 6 for stern trawlers. The number of seals feeding directly from the net while hauling was similar for both types of trawl vessel (T = -1.66, p = 0.099, df = 105) (present study).

Deep sea trawlers generally use 110 mm codend mesh in the survey area, except when targeting horse mackerel (85–90 mm) (Peter Sims, pers. comm.). Although seals are unable to pull large fish from the nets, smaller fish, and the heads/tails of large hake and kingklip which protrude from the net (stickers), are taken. Fish that float free from the net are also consumed by seals (present study). Loss of fish, and damage to fish, causes some loss of revenue to fishermen. However, considering that hauls range from 1/2 ton to 30 tons, depredation and damage by seals is negligible.

Losses are presumably higher for side trawlers. The reason for this is because during side trawl operations, the catch lies at the surface for some time while the codend is split and loaded over the side of the vessel. This allows time (*c*. 20 minutes) for seals to feed from the net. In contrast, stern trawlers haul the catch straight up the stern ramp, therefore there is minimal time (*c*. 5 minutes) for seals to feed from the net.

Number of seals feeding on offal and discarded by-catch

On the Eastern Cape coast, at least one seal was observed feeding on discarded offal/by-catch during most hauls. The mean number of seals feeding on offal/by-catch was 11 for side trawlers, and 6 for stern trawlers. The number of seals feeding on offal/by-catch was significantly higher for side trawlers ($T = 3.49$, $p = 0.001$, $df = 177$) (present study).

Soon after the net it brought aboard the vessel, the catch is processed. This involves discarding certain by-catch species which are of little/no value to the industry, and discarding offal (fish guts, fish heads, and trimmings). Seals are attracted to the net by the sound of the winch when hauling. When the net is at the surface, seals feed directly from the net. When the net is aboard, the seals remain near the vessel feeding on discards.

Damage to equipment

In this study, seals did not directly damage (tear) nets. However, on one occasion, two entrapped seals were cut from the net and released alive (present study).

Other observations indicate that seals do occasionally tear the net when attempting to free themselves, however damage is usually minor (Wickens, 1994).

Disturbance to operations

In this study, there was only one case where a seal was trapped in the factory area. Operations stopped for *c*. 10 minutes, after which time the seal was killed. On the west coast, Wickens (1994) reported two cases where a seal was trapped in the factory area of commercial trawlers ($n = 185$ trawls). On the south coast, Shaughnessy & Payne (1979) reported four cases ($n = 129$ trawls).

A loose seal trapped in the factory of a trawler is potentially dangerous, especially when it is a large adult male. Therefore, at least some of the crew must stop work until the animal is removed (or killed). This results in lost fishing time.

Seal mortality or injury

Number of seals incidentally entrapped in the net

On the Eastern Cape coast, the mean number of seals entrapped in nets was 30 per 100 trawls for side trawlers, and 21 per 100 trawls for stern trawlers. The maximum number of seals entrapped during a single trawl was 7. Side trawlers are more likely than stern trawlers to catch at least one seal per trip ($Z = 1.96$, $P = 0.050$) (present study).

The mean number of Cape fur seals entrapped in commercial trawl nets, per 100 trawls, in other areas is: 8.2 seals for the south coast, and 8.0 seals for the west coast (Shaughnessy & Payne, 1979). Thus, the frequency of entrapment for the Eastern Cape coast is comparatively high (present study).

Number of seals that incidentally drowned in the net

On the Eastern Cape coast, the mean number of seals incidentally drown was 17 per 100 trawls for side trawlers, and 10 per 100 trawls for stern trawlers. The maximum number of seals that had drowned in a single trawl was two. The likelihood of entrapping at least one drowned seal per trip is the same for side and stern trawlers ($Z = 1.52$, $p = 0.130$) (present study).

The mean number of Cape fur seals incidentally drowned in commercial trawl nets, per 100 trawls, in other areas is: 3.2 seals (Shaughnessy & Payne, 1979) and 5 seals (inshore trawlers) (Wickens, 1994) for the south coast; and 4.6 seals (Shaughnessy & Payne, 1979), and 1.6 seals (offshore trawlers) (Wickens, 1994) for the west coast. Thus, the frequency of drowning for the Eastern Cape coast is comparatively high (present study).

Number of seals deliberately killed by the captain/crew

When seals become trapped below the deck (in the factory area) they are often deliberately killed because they are potentially harmful to the crew, and difficult to remove.

On the Eastern Cape coast, the mean number of seals deliberately killed by the crew was one for stern trawlers (1.02 seals per 100 trawls) and nil for side

Table 11(a).25 *Entrapment of Cape fur seals incidental to trawling by commercial vessels off the Eastern Cape coast of South Africa.*

Year	Estimated no.of trawls[1] per depth zone (m)			Total estimated no. of trawls[1]	Estimated no. of seals caught in trawl nets	Estimated no. of seals drowned trawl nets	Estimated no. of seals drowned in trawl nets & deliberately killed
	≤ 100	**101–200**	**201–300**				
1992	1295	2797	19	4111	1061	563	584
1993	1333	2804	104	4241	1094	581	602
1994	1047	2399	103	3549	916	486	504
1995	1295	2124	139	3558	918	487	505
mean ± SE	**1243 ± 66**	**2531 ± 165**	**91 ± 25**	**3865 ± 182**	**997 ± 47**	**529 ± 25**	**549 ± 26**

[1] The number of trawls per year and depth zone completed by the inshore fleet to the east of 24º E, between 1992 and 1995 (Robert Leslie, pers. comm.).

trawlers (present study). The mean number of Cape fur seals entrapped in commercial trawl nets, per 100 trawls, in other areas is: 1.8 for the south coast (Shaughnessy & Payne, 1979); and 0.5 seals on the west coast (Wickens, 1994). Thus, the frequency of deliberate killing is negligible for all areas.

Overall seal mortality

Considering that the minimum mean distance travelled when trawling was similar for both side and stern trawlers (T = 0.01, p = 0. 992, *n* = 161); and that the number of trawls observed aboard side and stern trawlers were similar (*n* = 94 and 102 trawls), it is possible to pool the data and estimate overall seal mortality for the Eastern Cape coast. From the observed entrapment rates of seals (0.258 seals per trawl), the annual number of seals entrapped and brought aboard by commercial trawlers was estimated to be 977. From the observed mortality rates of seals due to drowning (0.137 seals per trawl), the annual mortality rate was estimated to be 529. From the observed overall mortality rates (0.142 seals drowned and deliberately killed per trawl), the annual overall mortality rate was estimated to be 549 (Table 11(a). 25).

Trawl depth

In the present study, 26 seals were drowned in commercial trawl nets (*n* = 190 trawls) (Appendix 11(a).1). Twenty one were entrapped towards the end of trawls (animals warm when on deck), and five were caught early in trawls (animals cold when on deck/signs of rigor mortis).

Commercial trawlers were operating between 106 m and 399 m, usually at 237 m (side trawler) and 203 m (stern trawlers). Cape fur seals can dive > 160 m. Therefore, seals are presumably entrapped when the net is held at ≤ 160 m. Although most animals were entrapped towards the end of trawls (when hauling), some animals entered the net when the net was deployed and/or being dragged along the sea bed.

In order to minimise the number of seals entrapped, trawlers should: (i) deploy the nets as quickly as possibly; (ii) trawl at depths > 160 m; and (iii) and retrieve the full net as quickly as possible.

Biology of drowned seals

The sex ratio of drowned animals was 1 female: 25 males. Counts of growth layer groups in thin tooth sections indicated that 23 of the drowned animals were ≥ 5 y. Three animals were of unknown age; however body length (curve) measurements suggested that they were all ≥ 5 y.

Most animals were in good physical condition, with blubber thickness ranging from 11.2–29.6 mm (mean 20.2 ± 1.4, *n* = 21). Five animals were slightly thin, with blubber thickness ranging from 6.0–7.6 mm (6.9 ± 0.3, *n* = 5).

Histological examination of the testis and epididymis indicated that all males collected between August and January were in reproductive condition, i.e., sperm observed in the epididymal tubules. Two of the six males collected in July had sperm in the epididymis. Males collected outside this period (between February and June) did not have sperm in the epididymis. Cape fur seals are seasonal breeders. The pupping/breeding season extends from November to late December. In most males, the testis regress between February and June, i.e, sperm is absent from the epididymis between February to June.

Examination of the reproductive tract of the female (PEM2012) indicated that she was also in reproductive condition. This animal was carrying a foetus measuring 42.5 cm (nose to tail) and weighing 3 123 g.

An additional 11 animals, drowned in nets off the Eastern Cape coast, were brought in by captains of the *Zuiderzee* and *Midharvid* (when the observer was not aboard the vessel) (Appendix 11(a).2). Counts of growth layer groups in thin tooth sections were made for five animals, all of which were ≥ 6 y. Standard body lengths of animals of unknown age suggested that these animals were all ≥ 5 y. Blubber thickness ranged from 17.0–39.9 mm (mean 28.0 ± 2.1, *n* = 10). One animal was slightly thin (blubber thickness 4.4 mm). All animals were male.

When all drowned animals are pooled (n = 37), two patterns are clearly evident. Firstly, animals are predominantly males, i.e., 1 female : 36 males. Secondly, animals were ≥ 5 y, i.e., 14 animals were 5–7 y (subadults); 12 were 8–9 y, and two were > 12 y (n = 28 canine aged animals). Examination of bacular length and canine age, suggested that about half of the animals had attained social maturity (8–10 y). Mean bacular length was 105.6 ± 2.2; range 85.9–136.1 (n = 34).

These results suggest that males are more likely to feed from trawl vessels than females; and males feeding from trawlers are generally older animals (≥ 5 y). Possible reasons for these observations are: older males have gradually learnt to associate trawl vessels with food; and younger males generally feed closer inshore, away from the offshore trawl grounds. These conclusions are in agreement with Oosthuizen (1991) who examined tagged Cape fur seals recovered at sea (seals drowned in fishing nets and shot for research).

CONCLUSION

On the Eastern Cape coast, some seals take fish from trawl nets, damage gear and disrupt fishing operations. Such interaction results in some loss of revenue to the fishermen; however, losses are negligible compared to the landed value of the fishery. Seals feeding from trawlers mainly consume stickers, fish floating free from the net, discarded by-catch and offal, thus loss and spoilage of fish is negligible. Sometimes fishermen have to cut the trawl net to free entrapped seals, but this cost is minimal. Occasionally a live seal is trapped in the factory area causing disruption and lost fishing time.

Cape fur seals are incidentally drowned in trawl nets, and are occasionally killed on vessels (when trapped in the factory area). The annual overall mortality rate (seals drowned and deliberately killed) for the Eastern Cape coast was estimated to be 549 seals. This mortality is negligible in comparison to the total population size (*c.* 1.5–2 million seals), and is likely to have little impact on the viability of the local population.

Cape fur seals are highly polygynous species, therefore only a small percentage of males reproduce. The removal of some ‘surplus’ males would not impact on the viability of the local population e.g., ‘territorial bulls’ were harvested for many years by Government Guano Islands, and then in the 1970s by private concessionaires, and the population continued to increase.

However, although this small seal population remains viable, the long term effects of changing the population structure, by removing males ≥ 5 years, are unknown. From a humanitarian view point, by-catch of any marine mammal is highly undesirable.

Future management studies should be concentrated in four key areas. Firstly, in order to prevent seals being entrapped in trawl nets, research is needed to develop effective non-lethal methods of deterring seals from fishing operations, e.g., deterrents to repel seals from fishing gear and/or conditioning seals to avoid fishing areas. Secondly, discarding of whole/parts of fish encourages seals to follow vessels. Therefore, efficient utilisation of/or disposal of offal and by-catch should be addressed. Thirdly, each vessel should be supplied with suitable equipment to capture and remove seals from the factory area. The market could subsidise such research by increasing the price of fish, and conservation organisations could assist with training crew on safe handling of seals. Finally, considering that large numbers of seals are being drowned in this area, on-going monitoring of the seal population is required.

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Appendix 11(a). 1 *Cape fur seals incidentally drowned in trawl nets off the Eastern Cape coast of South Africa between 1992 and 1995. Seals collected by independent observer aboard commercial trawl vessels (n = 196 trawls)*

	Accession no.	Date caught	Time caught (hrs)	Location	Trawl vessel (trip no., haul no.)	Trawl depth (m)	Dead seal on deck (W/C)[1]	Sex	Curve body length[2] (cm)	Blubber thickness[3] (mm)	Age[4] (y)	Sperm (Absent/ Present)	Testis weight (g)	Bacular length (mm)
1	PEM1999	20 Jul 1992	1040– 1400	34°52' 23°35'– 34°50' 23°48'	side (1, 2)	194	W	M	155	6.3	5	P	21.6/21.4	105.4
2	PEM2000	21 Jul 1992	0700– 1020	34°50' 23°48'– 34°48' 24°00'	side (1, 4)	188	C	M	146	6.0	5	A	21.5/19.3	89.4
3	PEM2001	21 Jul 1992	0700– 1020	34°50' 23°48'– 34°48' 24°00'	side (1, 4)	188	W	M	144	7.0	7	A	25.5/24.3	90.1
4	PEM2002	22 Jul 1992	1432– 1815	34°55' 23°14'– 34°53' 23°26'	side (1, 9)	192	W	M	163	7.6	8	A	30.6/28.5	121.0
5	PEM2003	24 Jul 1992	1145– 1445	34°51' 23°42'– 34°49' 23°53'	side (1, 12)	192	W	M	145	12.0	6	A	27.7/26.7	96.7
6	PEM2004	25 Jul 1992	1025– 1525	34°45' 24°18'– 34°48' 24°00'	side (1, 15)	210	W	M	194	18.0	> 12	P	44.9/41.6	112.1
7	PEM2005	11 Aug 1992	1545– 1905	34°43' 24°34'– 34°40' 24°45'	side (2, 19)	241	W	M	145	7.4	7	P	36.7/36.1	104.0
8	PEM2006	13 Aug 1992	1240– 1550	34°45' 24°25'– 34°42' 24°40'	side (2, 25)	313	W	M	153	13.3	7	P	31.7/29.7	99.3
9	PEM2007	14 Aug 1992	0955– 1300	34°42' 24°51'– 34°42' 24°42'	side (2, 27)	326	W	M	182	22.0	9	P	33.8/32.4	115.5
10	PEM2008	14 Aug 1992	1310– 1600	34°41' 24°42'– 34°38' 24°54'	side (2, 28)	278	W	M	147	29.4	–	P	28.2/27.6	121.1
11	PEM2009	22 Aug 1992	0645– 1026	34°47' 24°11'– 34°46' 24°25'	side (3, 42)	274	C (15.8°C)	M	148	11.2	5	P	24.5/23.3	96.6
12	PEM2010	22 Aug 1992	1100– 1445	34°45' 24°29'– 34°41' 24°45'	side (3, 43)	357	W (30.8°C)	M	147	11.3	7	P	28.7/25.9	85.9
13	PEM2011	8 Sep 1992	1443– 1800	33°50' 27°06'– 34°37' 24°59'	stern (1, 9)	183	W	M	160	11.8	–	P	31.8/30.7	92.3
14	PEM2012	9 Sep 1992	0630– 0900	34°40' 24°41'– 34°39' 24°53'	stern (1, 10)	186	C	F	162	29.3	–	_	–	–
15	PEM2013	13 Sep 1992	1410– 1800	34°24' 25°50'– 34°25' 26°02'	stern (1, 26)	139	C	M	166	18.7	8	P	28.1/27.7	–
16	PEM2014	25 Sep 1992	1450– 1830	34°23' 26°04'– 34°23' 25°58'	stern (1, 71)	142	W	M	162	22.0	7	P	38.8/–	97.2
17	PEM2015	3 Nov 1992	0630– 0900	34°17' 24°36'– 34°20' 24°23'	side (4, 57)	113	W	M	158	22.5	> 12	P	36.7/34.3	–

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	Accession no.	Date caught	Time caught (hrs)	Location	Trawl vessel (trip no., haul no.)	Trawl depth (m)	Dead seal on deck (W/C)[1]	Sex	Curve body length[2] (cm)	Blubber thickness[3] (mm)	Age[4] (y)	Sperm (Absent/ Present)	Testis weight (g)	Bacular length (mm)
18	PEM2046	19 May 1993	1017– 1400	35°00’ 21°41’– 35°08’ 21°27’	side (5, 81)	106	C	M	– (141)	11.7	7	A	21.4/19.2	105.4
19	PEM2047	20 May 1993	0630– 1000	34°53’ 23°27’– 34°50’ 23°40’	side (5, 83)	187	W	M	_ (167)	23.5	7	A	20.9/20.3	104.9
20	PEM2048	20 May 1993	0630– 1000	34°53’ 23°27’– 34°50’ 23°40’	side (5, 83)	187	W	M	– (157)	18.0	8	A	23.1/22.1	94.6
21	PEM2051	28 Jun 1993	1230– 1425	34°44’ 24°28’– 34°45’ 24°19’	stern (2, 91)	202	W	M	174 (168)	20.0	8	A	25.6/25.0	107.2
22	PEM2052	28 Jun 1993	1230– 1425	34°44’ 24°28’– 34°45’ 24°19’	stern (2, 91)	202	W	M	_ (171)	22.0	7	A	21.7/21.3	115.0
23	PEM2053	28 Jun 1993	1515– 1730	34°46’ 24°21’– 34°44’ 24°31’	stern (2, 92)	293	W	M	158 (153)	24.5	7	A	22.2/22.0	93.3
24	PEM2054	29 Jun 1993	1140– 1400	34°44’ 24°27’– 34°47’ 24°17’	stern (2, 94)	315	W	M	183 (165)	29.6	9	A	30.8/28.6	111.3
25	PEM2055	29 Jun 1993	1555– 1755	34°45’ 24°21’– 34°43’ 24°32’	stern (2, 95)	269	W	M	191 (179)	26.8	8	A	17.9/17.4	104.9
26	PEM2056	29 Jun 1993	1555– 1755	34°45’ 24°21’– 34°43’ 24°32’	stern (2, 95)	269	W	M	150 (139)	26.8	8	A	22.2/21.9	118.0

[1] W, dead seal warm on deck; C, dead seal cold on deck.

[2] In rough sea conditions it was not always possible to record SBL, therefore curve body length was taken with the animal lying on its back. SBL is given in round brackets when recorded.

[3] Blubber thickness taken at the base of the sternum.

[4] Age inferred from growth layer groups in the dentine of thin tooth sections.

Note, animals could not be weighed aboard the vessels.

Appendix 11(a). 2 ***Cape fur seals incidentally drowned in trawl nets off the Eastern Cape coast of South Africa between July 1993 and August 1995.*** **These animals were collected by the ship's captain (no independent observed aboard) and taken to the Port Elizabeth Museum for biological examination.**

	Accession no.	Date caught	Trawl vessel	Sex	Body length[1] (cm)	Body mass (kg)	Blubber thickness[2] (mm)	Age[3] (y)	Bacular length (mm)
1	PEM2082	19–20 Jul 1993	side	M	182 (176)	116	30.0	9	124.3
2	PEM2252	22–25 Aug 1994	stern	M	196[4] (172)	106	25.6	9	116.4
3	PEM2253	27–29 Aug 1994	side	M	166 (152)	86	33.0	–	113.6
4	PEM2254	27–29 Aug 1994	side	M	155 (146)	71	33.4	–	88.4
5	PEM2256	17–20 Sep 1994	stern	M	211[4] (198)	183	4.48	–	136.1
6	PEM2258	8–10 Oct 1994	stern	M	199 (186)	143	29.9	8	117.9
7	PEM2257A	19–22 Sep 1994	stern	M	159 (142)	73	17.0	6	96.2
8	PEM2257B	7–10 Oct 1994	stern	M	195 (170)	128	39.9	9	123.6
9	PEM2400	13–17 Jul 1995	stern	M	– (176)	97	26.0	–	110.3
10	PEM2401	13–17 Jul 1995	stern	M	161 (146)	69	22.6	–	88.2
11	PEM2414	25 Aug 1995	stern	M	151 (148)	58	22.3	–	95.0

Animals could not be weighed aboard the vessels.

[1] Body length was taken with the animal lying on its back. SBL is given in round brackets.

[2] Blubber thickness taken at the base of the sternum.

[3] Age inferred from growth layer groups in the dentine of thin tooth sections.

[4] Animals PEM2252 and PEM2256 were bloated.

CHAPTER 11(b)

Operational interactions between Cape fur seals *Arctocephalus pusillus pusillus* and fisheries off the Eastern Cape coast of South Africa: part two, squid jigging and line fishing

INTRODUCTION

The "inshore" fishing area off the south and east coasts of South Africa extends from Cape Agulhas (20° E) in the west, to the Great Fish River (27°10' E) in the east, and seawards to the 110 m depth contour (Appendix 11(b).1). The main commercial fisheries based in this region are inshore bottom trawling, squid jigging, hand-line fishing, and hake-directed longline (experimental fishery commenced in 1994) (Peter Sims, pers. comm.).

Recently fishing effort in Eastern Cape waters (Plettenberg Bay, 33° 07'S, 23°25'E, to the Kwazulu-Natal boarder, 31°05'S, 30°11'E) has increased significantly, particularly that for line fish and chokker squid. In 1992–1995, 234–254 squid vessels and 403–438 line fish vessels operated between Port Alfred and Mossel Bay[1]. White squid grossed between R46,236,024.00–R118,909,710.00 per annum, and line fish grossed between R9,459, 522.00–R16,600,173.00 per annum[1] (Chris Wilke, pers. comm.).

The main line fish species in this region are hake (*Merluccius* sp.), silver fish (*Argyrozona argyrozona*), panga (*Pterogymnus laniarius*), geelbek (*Atractoscion aequidens*), kob (*Argyrosomus hololepidotus*), yellowtail (*Seriola lalandi*), santer (*Cheimerius nufar*), red steenbras (*Petrus rupestris*), Cape gurnard (*Chelidonichthys capensis*), red stumpnose (*Chrysoblephus gibbiceps*), roman (*Chrysoblephus laticeps*), dageraad (*Chrysoblephus cristiceps*), mackerel (*Scomber japonicus*) and elf (*Pomatomus saltatrix*) (*Karina Vermaak, pers. comm.*). Snoek (*Thyrsites atun*) and kingklip (*Genypterus capensis*) are also targeted, mainly near Plettenberg Bay. The main target species for the squid jigging industry is chokker squid (*Loligo vulgaris reynaudii*) (Peter Sims, pers. comm.).

East coast fishermen operate in an area inhabited by Cape fur seals. At the time of this study, *c.* 140 000 Cape fur seals[2] (8.5% of the total population) inhabited the south/east coast, between False Bay and Algoa Bay, at five breeding colonies and one haul-out site (J.H.M. David, pers. comm.). Considering that some of the species eaten by Cape fur seals are of commercial importance (chapter 9), it is inevitable that seals and fisheries will come into conflict when fishing.

Some squid jig/line fishermen complain that seals: consume large quantities of commercially important species which would otherwise be available to the industry; take squid/fish from lines; break lines and tackle; and disperse schools from under the boat. Subsequently, many of these fishermen have a strong antipathy towards seals, and feel that the seal population should be reduced.

Many fishermen deliberately kill (shoot) seals to reduce their perceived impact. The effects of this on the local seal population are unknown, but unlike the west coast population, that on the Eastern Cape coast is not increasing.

Research examining operational interactions between seals and the line fish sector has been conducted on the west and south coast of southern Africa (Rand, 1959; Shaughnessy, 1985; Anon, 1987; Wickens, 1989; Meÿer *et. al.,* 1992; Wickens *et. al.,* 1992; Wickens, 1994); however, there is no comprehensive information for the Eastern Cape coast.

This study documents an evaluation of operational interactions between the squid jigging/line fishing industry and Cape fur seals, in waters off the Eastern Cape coast of Southern Africa. Information was obtained from questionnaire surveys, with limited independent observation aboard commercial chokker squid vessels (n = 31 days).

METHODS

In 1995 questionnaires (100 in total) were distributed to skippers of squid jig and line fish vessels, in the Eastern Cape coast of South Africa (Plettenberg Bay to Port Alfred) to obtain an indication of the nature and extent of seal-fisheries interactions.

Questions focused on five key areas: (i) fishing operations (target species; main fishing locations; fishing depth; number of fishing trips per year; duration of trip; number of lines operated); (ii) seal attendance; (iii) depredation and damage to equipment (catch losses; gear damage; operational disturbance); (iv) seal mortality (methods used to remove seals from the area; deliberate shooting of seals); and (v) general attitude of fisherman towards seals.

Fifty seven replies were received, 48 of which are presented in this study. Thirty three of the 48 replies were from skippers of commercial squid jig vessels, some of whom also held a permit to target teleost fish. The remainder were from skippers of commercial and semi-commercial line fish vessels.

Information on seal-fisheries interactions within the squid jig industry was also collected by an independent observer (Willie de Wet). These direct observations were used to substantiate responses in the questionnaire surveys. Independent observations were conducted in 1995, between June and November, over a 31 day period. Observations were made from four commercial squid jig vessels (*Dereck, Peregrine, Queen Cat* and the *King Cat*). These vessels were 15–20 m in length. Crew size was *c.* 25.

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[1] This data was extracted from the National Marine Linefish System (NMLS) based on data provided by the permit holders on a monthly basis.

[2] Inferred from pup counts for 1993.

For the purpose of this study, responses from the squid jig skippers and line fish skippers are presented separately. Means are always followed by the standard error. The number of skippers that responded to each question, *n*, is given round brackets.

RESULTS

Handline jigging for chokker squid (questionnaire)

Fishing operations

Skippers participating in questionnaires operated between Cape Agulhas Point (grid 535) and Mbashe Point (grid 671), with fishing effort concentrated between Plettenberg Bay and Cape St Francis (grids 516–520), and between Cape Recife and Great Fish Point (grids 625, 628, 632, 636, 640, 644) (*n* = 33 skippers) (Appendix 11(b).2). Several skippers operating in this region also fished as far west as Cape Agulhas Point.

Fishing depth ranged from 0–150 m, with mean[3] depth at *c.* 45 m. The mean[3] number of lines per vessel was *c.* 35 (range 4–75 lines). The mean[3] number of fishing trips was *c.* 75 (range 10–300 trips). The mean[3] duration of fishing trips was *c.* 14 hrs (range 4–28 hrs).

Seal attendance

How many seals are usually observed in the vicinity of lines while fishing?

The mean number of seals usually observed in the vicinity of lines while fishing was 3.1 ± 0.3; range 1–7 (*n* = 33 skippers) (Table 11(b).1).

Are seals more abundant in certain fishing locations?

Table 11(b).1 *Number of seals usually observed in the vicinity of lines while fishing (n = 33 skippers)*

No. of seals	Count	Percent
1	1	3.0
2	12	36.4
3	12	36.4
4	5	15.2
7	3	9.1
	33	

Eighty three percent of skippers reported that seals were more abundant in certain fishing locations (*n* = 30 skippers).

Seals were reported to be more abundant from Elands Point to Bird Island/Cannon Rocks (especially in grids 532–534, 625 and 636). Other 'seal hot spots' included Plettenberg Bay to Keurboom; Natures Valley, Eerste Rivier, Oubos to Aasvoël Punt; and Jeffreys Bay.

Selected comments from skippers included:

> *..."seals are normally found in the deeper fishing areas"...*
>
> *..."numbers vary due to changes in fish concentrations"...*

Are seals a greater problem at certain months of the year?

Fifty eight percent of skippers reported that seal-fisheries problems increased at certain months of the year (*n* = 24 skippers).

Of the 14 skippers whom reported that seals were more of a problem at certain months of the year, 78% reported that seal-fisheries problems increased between April and August (Table 11(b).2).

Selected comments from skippers included:

> *..."seals are a problem especially when fishing under lights at night during the winter months when groups of 5–10 seals are often encountered in the deeper water from 40–90 m"...*

Table 11(b).2 *Months of the year in which seals are a greater problem to the squid jig fishery (n = 14 skippers)*

Season	Month	Count	Percent
Summer	12	3	6.7
	1	2	4.4
	2	1	2.2
Autumn	3	0	0
	4	5	11.1
	5	8	17.8
Winter	6	11	24.4
	7	6	13.3
	8	5	11.1
Spring	9	1	2.2
	10	1	2.2
	11	2	4.4
		45	

Depredation and damage to equipment

Do seals interfere with your fishing operations?

Thirteen percent of skippers reported that seals sometimes interfered with their fishing operations, however they caused little disruption or damage; 34% reported that seals frequently interfered, however they consider seals to be a minor problem; and 53% reported that seals frequently interfered, and they consider seals to be a major problem (*n* = 32 skippers).

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[3] Squid jig fisherman either stated a range (minimum value to maximum value), or gave an estimated mean. Therefore, an overall mean was calculated using the minimum and the maximum values, as well as the estimated mean.

What are the adverse effects of interactions with seals on the squid jig fishery?

Skippers reported that seals scatter schools of squid, take squid from lines as they are being hauled to the surface, and break lines/tackle (*n* = 33 skippers) (Table 11(b). 3).

Table 1(b).3 ***Adverse effects of interactions with seals on the squid jig fishery (n = 33 skippers)***

Seal-fisheries interactions	Count	Percent
Scatter schools of squid	3	9.1
Take squid from lines	3	9.1
Break lines/tackle	4	12.1
Scatter schools of squid & take squid from line	5	15.2
Scatter schools of squid & break lines/tackle	2	6.6
Break lines/tackle & take squid from lines	5	15.2
Scatter schools of squid & take squid from lines & break lines/tackle	11	33.3
	33	

How often do seals break your lines?

About half of the skippers reported that seals often break lines, while half reported that seals seldom break lines (*n* = 29 skippers) (Table 11(b).4).

Table 11(b).4 ***Line breakage attributed to interaction with seals (n = 29 skippers)***

Seals beak fishing lines	Count	Percent
Never	0	0
Seldom	13	44.8
Often	15	51.7
Always	1	3.5
	29	

How often do seals cause the squid to scatter?

Eighty two percent of skippers reported that seals often/always cause squid schools to scatter during fishing operations (*n* = 28 skippers) (Table 11(b).5).

Selected comments from skippers included:

…"Seals scatter schools of squid, mainly at night when they disrupt bait fish which the squid feed on"…

…"They make the schools of squid sound, thereby slowing down the catch rate considerably until the seals leave the area or are shot"…

Table 11(b).5 ***How often do seals cause squid schools to scatter (n = 28 skippers)***

How often seals scatter squid schools	Count	Percent
Never	1	3.6
Seldom	4	14.3
Often	15	53.6
Always	8	28.6
	28	

How many squid on average would you loose per trip in comparison with your total catch ?

Seventy eight percent of skippers reported that seals took 5% to < 20% of the total catch from their lines (*n* = 27) (Table 11(b).6).

Selected comments from skippers included:…"

…Seals take squid from the line "0% to < 5% at day time and 5% to < 10% at night. They can be totally disruptive in schools at night"…

.."Not sure. The problem is not the number taken from lines but the loss of fish/squid under the boat"…

…"Sometimes seals take squid from lines, bite it dead but do not eat it. It's like a game - it comes back to do it over and over"…

Table 11(b). 6 ***Percentage of the total catch lost due to seals taking squid from the lines (n = 27 skippers)***

Percent of total catch lost to seals	Count	Percent
< 5%	0	0
5% to < 10%	13	48.2
10 % to < 20%	6	22.2
20% to < 50%	5	18.5
> 50%	3	11.1
	27	

What is the economic impact of seals taking squid from lines?

Sixty seven percent of skippers reported that seals taking squid from lines caused considerable economic loss to their fishing operations (*n* = 30 skippers).

Seal mortality or injury

Do you attempt to remove the seals from your area?

Sixty percent of skippers (18) endeavour to remove seals from the area during fishing operations (*n* = 30 skippers). However, this figure is larger considering that 25 fishermen listed actual methods used to remove seals from their fishing operations (see below).

Selected comments from skippers included:

…"At times seals can be very disruptive. On occasions they cause serious loss of catch and tackle. This occurs mostly in winter and at night under lights. Its only under those conditions that action is taken against seals"…

… "I try to avoid shooting seals in fear of fouling squid breeding grounds with carcasses which might attract sharks"…

How do you prevent seals from interfering with fishing operations?

The main method employed to discourage seals from interfering with fishing operations was to use a shot gun, i.e., shoot near the seal to frighten it and/or shoot to kill (Table 11(b).7). Other methods reported by skippers included: *"gaffing the seals"; "using knives"; "throwing objects at them to chase them away"; "throwing sinkers"; "catching them" and "waiting for some other idiot to shoot them usually by shot gun".* Rifles and clubs were used by several fishermen.

Table 11(b).7 ***Methods used to prevent seals from interfering with fishing operations (n = 27 skippers)***

Method used to deter seals	**Count**	**Percent used**
Rifle	2	7.4
Shot gun	13	48.1
Club	3	11.1
Other methods	6	22.2
Shot gun & other methods	1	3.7
Do not intervene[1]	2	7.4
	27	

[1] Move away to another location or stop fishing until the seals move on to another vessel.

How many seals do you shoot per year?

The mean number of seals shot per year was 45.8 ± 24.9 (range 0–480, *n* = 20 skippers). The minimum and maximum number of seals shot per year were 2.4 ± 1.4 (range 0–10) and 11.9 ± 6.5 (range 2–50), respectively (*n* = 7 skippers).

Thirteen skippers provided estimates of the number of seals that they shot each year (Table 11(b).8).

Table 11(b).8 ***Mean number of seals shot by fishermen (n = 13 skippers)***

Fishing grid no.[1]	**No. seals shot per year**
–	0–3
636–637, 640, 644	0–5
516–518, 519	0–10
632, 636, 640	1–2
–	2–3
518–520	5
516, 519–520, 625, 628, 636, 640, 644	4–10
516–644	10–50
616, 518–520, 532–534, 622, 625, 628–629, 632, 636, 640, 644–645	100
516–517, 519, 520	100
516	100[2]
516	130[2]
516	480[2]
	***c.* 900–1000**

[1] Main fishing locations of individual skippers.

[2] Plettenberg Bay (hake and squid jig fishermen).

Attitude of fishermen towards seals

What is the general feeling of the local fishing community towards seals?

Forty three percent of skippers reported that seals were too numerous and should be managed to prevent negative interactions with the fishing community (*n* = 31 skippers) (Table 11(b).9).

Table 11(b).9 ***General attitude of local squid jig fishermen towards seals (n = 31 skippers)***

Attitude of fishermen towards seals	**Count**	**Percent**
A	6	13.6
B	11	25.0
C	8	18.2
D	19	43.2
	44*	

A, seals do not significantly interfere with fishing operations. B, seals are a major problem to the squid jig fishery. Seals take squid from lines and damage gear. C, seals compete with the local fisheries because they feed on commercially important species, thus reduce the potential catch of fishermen. D, seals are too numerous and should be managed to prevent negative interactions with the fishing community.

* Several fishermen gave more than one answer.

Selected negative comments from skippers included:

..."Fishermen generally hate seals and thus shoot them with shotguns"...

..."They are a menace in the ocean and should be culled"...

..."The seals overpopulation is a MAN created problem thus should be remedied by MAN"...

..."The scientists are very concerned to protect the fishing resource by introducing size limits, closed seasons etc. They will achieve their goal a lot more successfully by reducing the seal population urgently"...

..."The presence of so many fishing vessels has upset the balance of nature. Not only the fittest survive - all survive by scavenging near boats. The seal population should be culled A.S.P. as their numbers are increasing on the east coast as well"...

Selected positive comments from skippers included:

..."We as fishermen do not want to interfere with seals as they find fish/squid very often for us. But they often scatter big schools of fish/squid. The general feeling for seals is not to hurt them but to try and chase them. A gun shot in the air does chase them very often"...

..."Seals can be a menace at times, however they can also help one in locating a school of squid. The only reason I may shoot the odd seal is when they are really destroying everything and the crew are upset and are about to jig them and kill them in a barbaric way"...

..."Sometimes we look for seals to find squid"...

...Don't kill the seals because they help us with our living on the waters"...

..."They don't interfere in any significant way but are mercilessly shot on sight by the majority of deck boat skippers. Seals should be protected in these parts"....

Handline jigging for chokker squid (independent observer)

Information collected on ‘fishery data sheets’ by an independent observer aboard commercial squid jig vessels has been summarised in Table 11(b).10.

Fishing operations

Mean fishing depth was 42.7 ± 2.7 m (range 22–70 m); the number of lines ranged from 23–31; and the duration of fishing trips was 5–8 days ($n = 5$ trips).

Seal attendance

During the 31 days at sea, seals were sighted near the vessel on 36 separate occasions. The mean number of seals near the vessel was 1.3 ± 0.1 (range 1–4).

Depredation and damage to equipment

When seals were near the vessel, seal-fisheries interactions were observed 47% of the time, i.e., seals were observed feeding on squid near the lines.

When feeding on squid, seals were observed taking squid directly from lines on four separate occasions. Although it was difficult to determine the number of squid taken from lines, estimated loses were: (i) 1–2 squid, (ii) 8 squid, (iii) > 1 squid and (iv) 1–2 squid, respectively.

Seals broke lines/tackle on three separate occasions. On the first occasion eight lines were broken. On the second and third occasion one line was broken.

Seals caused squid to disperse[4] totally from the area once, when 4 seals were around the vessel.

Table 11(b).10 ***Summary of interactions that occur between seals and squid jig fishermen on the Eastern Cape coast of South Africa: independent observation aboard commercial vessels over a 31 day period***

Date	Local time (hrs)	Fishing location	Fishing depth (m)	No. seals at lines	Seal-fisheries interaction					Shooting of seals
					A	B	C	D	E	
22 Jun 95	2112	33°56’S 25°44’E	38.6	2		+	+			shot gun
22 Jun 95	0300	33°56’S 25°44’E	38.6	1		+	+	+		shot gun
24 Jun 95	2041	33°56’S 25°44’E	43.7	1		+				shot gun
24 Jun 95	0245	33°56’S 25°44’E	43.7	1		+	+	+		shot gun
23 Jul 95	2300	33°56’S 25°44’E	70.0	1	+					
24 Jul 95	1045	34°02’S 25°05’E	46.0	1	+					
24 Jul 95	2000	34°09’S 25°03’E	62.0	1		+				
25 Jul 95	1131	34°12’S 24°56’E	62.0	1	+					
25 Jul 95	1300	34°12’S 24°56’E	62.0	2	+					
25 Jul 95	1400	34°12’S 24°56’E	62.0	1	+					
26 Jul 95	1130	34°12’S 24°56’E	66.0	1	+					
28 Jul 95	1945	34°09’S 24°59’E	56.6	1	+					
28 Aug 95	0900	Maitland	66.0	1		+				shot gun
28 Aug 95	1730	Maitland	66.0	1	+					shot gun
29 Aug 95	0745	Maitland	66.0	1	+					
29 Aug 95	1130	–	52.0	1	+					
30 Aug 95	2030	34°05’S 25°01’E	54.0	1	+					shot gun
30 Aug 95	2108	34°05’S 25°01’E	54.0	1	+					shot gun
31 Aug 95	0915	–	54.0	1		+				
19 Oct 95	0800	33°44’S 26°03’E	31.1	1		?				
19 Oct 95	0915	33°44’S 26°03’E	32.9	1	+					
19 Oct 95	1705	33°44’S 26°03’E	32.0	1	+					shot gun
20 Oct 95	0613	33°44’S 26°03’E	31.1	1		+				shot gun
20 Oct 95	0630	33°44’S 26°03’E	31.1	1	+					
20 Oct 95	0711	33°44’S 26°03’E	31.1	1	+					
20 Oct 95	0720	33°44’S 26°03’E	31.1	1		+	+	+		shot gun
20 Oct 95	1200	33°44’S 26°03’E	31.1	1	+					rifle*
20 Oct 95	1710	33°44’S 26°03’E	31.1	1	+					rifle*
20 Oct 95	2130	33°44’S 26°03’E	29.3	1		+				shot gun
22 Oct 95	1001	33°59’S 25°13’E	22.6	5		+				shot gun
22 Oct 95	1709	33°59’S 25°13’E	22.6	2		+				shot gun
24 Oct 95	1009	34°00’S 25°17’E	23.8	1		+				shot gun
24 Oct 95	1408	34°00’S 25°17’E	23.8	1	+					
2 Nov 95	1800–	34°01’S 25°15’E	24.1	4		+			+	shot gun
3 Nov 95	1540 1900	33°59’S 25°13’E	21.9	1		+				
3 Nov 95	1735	33°59’S 25°13’E	21.9	1		+				shot gun
				1–5	**19**	**16–17**	**4**	**3**	**1**	**19**

Start and end date of each of the 5 trips: (i) 21 Jun 95–25 Jun 95; (ii) 23 Jul 95–29 Jul 95; (iii) 27 Aug 95–1 Sep 95; (iv) 18 Oct 95–25 Oct 95; and (v) 30 Oct 95–4 Nov 95.

A, no interaction or no obvious interaction with fishing operations; B, feeding on squid at vessel; C, take fish from lines; D, break line and tackle; E, seals cause schools to totally disperse from area.

* Rifle obtained from neighbouring vessel.

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[4] Furthermore, on October 22, 1995 at Beachview, dolphins caused squid to totally disperse from the area on three occasions, i.e., no signs of squid on the echo.

Table 11(b). 11 ***Main specie of line fish targeted off the Eastern Cape coast (n = 15 skippers)***

	Common name	**Scientific name**	**Count**	**Percent**
1	Stock fish (hake),	*Merluccius capensis & M. paradoxus*	12	27.3
2	Carpenter (silverfish)	*Argyrozona argyrozona*	8	18.2
3	True kob (kabeljou)	*Argyrosomus hololepidotus*	7	15.9
4	Geelbek	*Atractoscion aequidens*	4	9.1
5	Yellow-fin tuna (& tuna[1])	*Thunnus albacares*	3	6.8
6	Santer	*Cheimerius nufar*	2	4.6
7	Dageraad	*Chrysoblephus cristiceps*	2	4.6
8	Roman	*Chrysoblephus laticeps*	1	2.3
9	Panga	*Pterogymnus laniarius*	1	2.3
10	Elf (shad)	*Pomatomus saltatrix*	1	2.3
11	Kingklip	*Genypterus capensis*	1	2.3
12	Dikbek (barred thick-lip)	*Hemigymnus* sp	1	2.3
13	Reds[2]		1	2.3
			44	

[1] Presumably yellow-fin tuna, striped bellied benito, big eye and blue fin tuna.

[2] Presumably capenter, santer, panga and roman.

One semi-commercial fisherman also reported salmon in grids 632–633.

Seal mortality or injury

When seals were near the vessel, fishermen shot seals 53% of the time to safeguard their catches. Seals were usually shot with a shot gun. A rifle was used on two occasions.

Line fishing for teleost fish (questionnaire)

Fishing operations

Main target species and corresponding fishing locations

Skippers participating in questionairres reported that 12 fish species were important to their fishing operations, particularly hake, carpenter and kob (*n* = 15 skippers) (Table 11(b).11). Fishing effort was concentrated between Cape Recife and Bird Island (grids 625–630 and 632–634), and between Knysna Heads and Elands Point (grids 515–518 and 529–531) (Appendix 11(b).3).

Fishing depth ranged from 14–115 m, with mean[5] depth at *c*. 80 m. The number of lines per vessel ranged from 1–16 lines). The mean[5] number of fishing trips was *c*. 80 (range 15–250 trips). The mean[5] duration of fishing trips was *c*. 10 hrs (range 5–12 hrs).

Seal attendance

How many seals are usually observed in the vicinity of lines while fishing?

The mean number of seals usually observed in the vicinity of lines while fishing was 3.1 ± 0.3; range 2–6 (Table 11(b).12).

Table 11(b).12 ***Number of seals usually observed in the vicinity of lines while fishing (n = 15 skippers)***

No. of seals	**Count**	**Percent**
2	6	40.0
3	4	26.7
4	4	26.7
6	1	6.7
	15	

Are seals more abundant in certain fishing locations?

Forty three percent of skippers reported that seals were more abundant in certain fishing locations (*n* = 14 skippers).

Six skippers listed areas where seals were more abundant (Table 11(b).13).

Table 11(b). 13 ***Fishing locations where seals are more abundant (n = 6 skippers)***

Fishing location	**Count**	**Percent**
515	1	7.7
516	1	7.7
529	1	7.7
530	1	7.7
625	3	23.1
626	2	15.4
629	2	15.4
630	1	7.7
633	1	7.7
	13	

Selected comments from skippers included:

…"Seal distribution varied occurring to fluctuation in fish concentrations"…

…"Seals were generally more common in stock fish grounds"…

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[5] Line fisherman either stated a range (minimum value to maximum value), or gave an estimated mean. Therefore, an overall mean was calculated using the minimum and the maximum values, as well as the estimated mean.

Depredation and damage to equipment

Do seals interfere with your fishing operations?

Seven percent of skippers reported that seals did not interfere with their fishing operations; 20% reported that seals sometimes interfered, however they caused little disruption or damage; 40% reported that seals frequently interfered, however they consider seals to be a minor problem; and 33% reported that seals frequently interfered, and they consider seals to be a major problem (n = 15 skippers).

What are the adverse effects of interactions with seals on the line fish sector?

Skippers reported that seals in this region scatter schools of fish, take fish from lines as they are being hauled to the surface, and break lines/tackle (n = 15 skippers) (Table 11(b).14).

Table 11(b).14 ***Adverse effects of interactions with seals on the hook and line fishery (n = 15 skippers)***

Seal-fisheries interactions	Count	Percent
Scatter schools of fish	1	6.7
Take fish from lines	6	40.0
Break lines/tackle	1	6.7
Scatter schools of fish & take fish from line	1	6.7
Break lines/tackle & take fish from lines	6	40.0
	15	

How often do seals break your lines?

Ninety one percent of skippers reported that seals seldom break fishing lines (n = 11 skippers) (Table 11(b).15).

Table 11(b).15 ***Line breakage attributed to interaction with seals (n = 11 skippers)***

Seals beak fishing lines	Count	Percent
Never	0	0
Seldom	10	90.9
Often	1	9.1
Always	0	0
	11	

How often do seals cause the fish to scatter?

Sixty percent of skippers reported that seals never, or seldom cause, fish schools to scatter during fishing operations (n = 10 skippers) (Table 11(b).16).

Table 11(b).16 ***How often do seals cause fish schools to scatter (n = 10 skippers)***

Seals scatter fish schools	Count	Percent
Never	2	20.0
Seldom	4	40.0
Often	4	40.0
Always	0	0.0
	10	

How many fish on average would you loose per trip in comparison with your total catch ?

Eighty percent of skippers reported that seals take < 10% of the total catch from lines (n = 10 skippers) (Table 11(b).17).

Selected comments from skippers included:

*…"It depends on the size of the seal. If a very large seal with a hairy neck (*large adult male*) is around the boat, then he will take all of the catch and completely stop you from fishing"…*

…"About 20% to 30% of times they really become pests, mainly taking soft fish, e.g., hake and carpenter from your line"…

…"Anything from 1 fish to total catch. The crew become despondent and will not fish. Moving a few miles does help but time is cost"…

Table 11(b).17 ***Percentage of the total catch lost due to seals taking fish from the lines (n = 10 skippers)***

Percent of total catch lost to seals	Count	Percent
< 5%	5	50
5% to <10%	3	30
10 % to <20%	2	20
20% to < 50%	0	0
> 50%	0	0
	10	

What is the economic impact of seals taking fish from lines?

Sixty four percent of skippers reported that seals taking fish from lines caused little economic loss to their fishing operations (n = 11 skippers).

Seal mortality or injury

Do you attempt to remove the seals from your area?

Fifty three percent of skippers (8) reported that they do attempt to remove seals from the area (n = 15 skippers). However, this figure is larger considering that 11 fishermen listed actual methods used to remove seals from their fishing operations (see below).

How do you prevent seals from interfering with fishing operations?

The main method employed to discourage seals from interfering with fishing operations was to use a shot gun, i.e., shoot near the seal to frighten it and/or shoot to kill (Table 11(b).18). Other methods reported by fishermen included: *"feeding the seals with mackerel"; "throwing stones"; "throwing sinkers attached to a line"; "shooting the seals with a catapult"; "loud noises"; "starting of engines"; "banging gaffs on the water surface" and "hooking seals"*. A club was used by one fishermen. Rifles were not used.

Table 11(b).18 ***Methods used to prevent seals from interfering with fishing operations (n = 14 skippers)***

Method used to deter seals	**Count**	**Percent**
Rifle	0	0.0
Shot gun	4	28.6
Club	1	7.1
Other methods	3	21.4
Do not intervene[1]	6	42.9
	14	

[1] Move away to another location or stop fishing until the seals move onto another vessel.

How many seals do you shoot per year?

The mean number of seals shot per year was 50.7 ± 34.9 (range 0–480, n = 14 skippers). The minimum and maximum number of seals shot per year ranged from 50–250 (*n* = 1 skipper).

Four skippers provided estimates of the number of seals that they shot each year (Table 11(b).19).

Table 11(b).19 ***Mean number of seals shot by fishermen (n = 4 skippers)***

Fishing grid no.[1]	**No. seals shot per year**
515–518, 529–532	50–250
516	100[2]
516	130[2]
516	480[2]
	***c.* 760–960**

[1] Main fishing locations of individual skippers.

[2] Plettenberg Bay (hake and squid jig fishermen).

General attitude of fishermen towards seals

What is the general feeling of the local fishing community towards seals?

Forty percent of skippers reported that seals are too numerous and should be managed to prevent negative interactions with the fishing community (*n* = 13 skippers) (Table 11(b).20).

Table 11(b).20 ***General attitude of line-fishermen towards seals (n = 13 skippers)***

Attitude of fishermen towards seals	**Count**	**Percent**
A	4	26.7
B	6	40.0
C	2	13.3
D	3	20.0
	15*	

A, seals do not significantly interfere with fishing operations. B, seals are a major problem to the line-fishing industry. Seals take fish from lines and damage gear. C, seals compete with the local fisheries because they feed on commercially important species, thus reduce the potential catch of fishermen. D, seals are too numerous and should be managed to prevent negative interactions with the fishing community.

* Two skippers gave 2 responses.

Selected comments from skippers included:
...*"Seals are basically a major problem...they are incredibly destructive...deepwater longliners suffer badly"...*
...*"Local fishermen generally complain about seals, but when you inquire, you find very few have actually lost fish/lines to seals. They are bothersome at times but can be scared off by loud noises and banging gaffs on the water surface when they are not deep down"...*

DISCUSSION

In waters off the Eastern Cape coast, interactions between the jig and line fishing industry, and Cape fur seals, can result in revenue losses to fishermen and mortality/injury to seals.

Seal attendance

Skippers reported that seals were nearly always present while fishing, and the average number of seals near lines was 3 (range 1–7) (present study). Independent observation aboard squid jig vessels suggested that this number was slightly lower, i.e, an average of 1.3; range 1–4 (present study). In comparison, independent observations on the west/south coast, suggest that an average of 1.5 seals (Meÿer *et al.*, 1992) or 2 seals (Wickens, 1994) are usually observed around handline vessels while fishing.

There was no obvious localised region of seal-fisheries interaction. However, many of the line fishermen reported that seals were usually more common in deeper waters, especially off the main headlands (Mossel Bay; Knysna Heads to Plettenberg Bay; and Cape Recife), and south-east of Bird Island. Squid jig fishermen also reported observing more seals near Plettenberg Bay, Cape Recife and the Bird Island area, and reported observing more seals in deeper waters between Elands Point and Cape St Francis.

Seal-fisheries interactions occurred at day and at night. East coast line fishermen are generally active during the day, and the squid jig fishermen are active at day and night. Squid jig fishermen reported that seals were particularly destructive at night when fishing under lights, especially in winter.

Although interaction with seals occur throughout the year, some fishermen report that interactions increase in April to August (especially in June), when the majority of seals are feeding at sea. Most squid is landed from June to December, which may partially explain the high incidence of interaction reported in the winter months. Seals come ashore in large numbers to give birth and mate in November and December, and to moult in January to March (Rand, 1967, David & Rand, 1986). From November to December, and possibly January to March, the majority of seals presumably feed less, and/or feed closer to breeding colonies, reducing interaction with fishermen on the main fishing grounds (Meÿer *et al.,* 1992).

Depredation and damage to equipment

Questionnaire surveys suggested that squid jig fishermen, and longliners targeting hake (Plettenberg Bay area), experienced greater conflict with seals than did other line fishermen. The majority of squid jig fishermen reported that seals often/always caused squid schools to scatter, whereas most line fishermen reported that seals never/seldom caused fish schools to scatter. Seals breaking lines was considered to be a problem on about half of the squid jig vessels, whereas most line fishermen reported that seals seldom broke lines. Taking fish from lines was of considerable economic loss to the majority of squid fishermen, but was of little economic loss to the majority of line fishermen.

Independent observation aboard squid jig vessels indicated that seals seldom broke lines/tackle, and seldom caused squid schools to disperse from the area (present study). When interaction was observed, seals were generally feeding near the lines, occasionally taking squid directly from the lines. The maximum number of squid taken directly from lines by a single seal was eight; and the maximum number of lines broken by a single seal was eight. These two examples indicate that seals can cause considerable disruption at times, resulting in financial loss to fishermen in terms of loss of tackle (e.g., nylon line, dollies, hooks, swivels and sinkers), lost fishing time, and loss of potential catch.

In comparison, independent observations on the west/south coast indicated that losses of fish and tackle to seals are of a relatively minor nature relative to the value of the handline fishery (Meÿer *et. al.,* 1992; Wickens, 1994); and seals occasionally scatter schools of fish, e.g., seals were thought to cause snoek schools to sound five times during 103 days of fishing (Meÿer *et. al.,* 1992); no cases of seals scattering fish schools were reported by Wickens (1994).

Deliberate killing (shooting) of seals

On the Eastern Cape coast, a minority of fishermen are responsible for killing large numbers of seals each year to safeguard catches. Seventeen skippers reported that they deliberately kill seals, i.e., four line fishermen kill a total of *c.* 760–960 seals per year; and 13 squid jig fishermen kill at total of *c.* 900–1000 per year. Three of these fishermen have a licence to fish for squid and hake, therefore seal mortality for the 14 fishermen was *c.* 810–1210 seals. Considering that there were 234–243 squid jig/403–438 line fishing vessels operating between Port Alfred and Mossel Bay between 1992 and 1995 (Chris Wilke, pers. comm.), overall mortality will be considerably higher.

Independent observation aboard squid jig vessels indicate that seals are often shot to safeguard catches, i.e., an average of 0.6 seals shot per day over the 31 day period. When one or more seals were observed near lines, action was taken to safeguard catches 53% of the time, i.e., 19 out of 36 observed cases. A shot gun was usually used to shoot seals, although a rifle was used on two occasions. On the west/south coast, independent observations also confirm that seals are deliberately shot by line fishermen, however the magnitude of the problem has not been quantified (Wickens, 1994).

Although deliberate killing of seals without a permit is illegal, it is almost impossible for Fisheries Control Officers to enforce this law across the entire region (see section 3b of the Seabirds and Seal Protection Act 46 of 1973). Until effective methods of deterring seals from fishing operations are developed, unfortunately the deliberate killing (shooting) of seals will continue. Therefore it must be done humanely. Although a variety of methods have been used to deters seals from fishing operations (including explosive firecrackers, electric pulses, air guns and sounds of killer whales), none have proven successful for all fisheries (Wickens *et al.,* 1992).

When shooting seals at sea, fishermen usually use a 12 bore shotgun. Rifles and pistols are less commonly used. Shooting in the air usually does not deter seals when feeding, therefore many fishermen shoot near or at the seal. At sea, it is not always possible to achieve a clean head shot because: the vessel is moving; seal movement is erratic; and the seals may be below the water surface. Therefore, many seals are shot in the stomach or back, and die a slow, painful death.

Examination of seals stranded along the Eastern Cape coast between January 1992 and December 1995 (n = 47 seals collected by Stewardson), indicated that 9 seals (19%) had been shot, presumably by fishermen (Appendix 11(b).4). These animals were all adult males with a mean standard body length of 171.6 ± 7.6 cm, range 145–216 cm. Only two seals had been shot in the head. The remainder were shot in the stomach, neck or between the shoulders.

Marksmanship, distance from the seal, and the type of projectile used, influence the likelihood of achieving a fatal wound. When using shot guns at sea, many fishermen are probably using small shot to ensure that at least some pellets hit the seal. Although a hit may frighten seals from the area, small shot is likely to cause injury and suffering. If seals must be shot (e.g., removing rogue bulls from the area), larger pellets travelling at least 1200 feet per second, preferably calibre .222 inches, should be used. Larger pellets penetrate deeper into the animal inflicting a fatal wound.

When using 303 rifles at sea, some fishermen may use sporting projectiles (soft point) to inflict a fatal wound. However, when shooting through water, this type of bullet will break up, and therefore injure (rather than kill) the animal. The use of military projectiles (full metal jackets) should be used to achieve a fatal wound. A .22 rifle is not powerful enough to kill an adult seal humanely, and therefore should not be used.

Other methods used to deter seals

Other methods used by fishermen to discourage seals from interfering in fishing operations included: firing a shot near the seal to frighten it; using clubs; gaffing/hooking the seal; using knives; throwing objects (e.g., sinkers, stones); using a catapult; feeding the seal with mackerel; catching the seal; loud noises; starting of engines; banging gaffs on the water surface; waiting for some other fishermen to shoot the seal; and moving to another area (present study).

On the west/south coast, handline fishermen also discourage seals from interfering in fishing operations by: using a catapult (to shoot stones or lead); gaffing the seal; and moving to another area (Wickens, 1994). In addition fishermen harpoon seals; move slowly past another boat in hope that the seal would follow that boat; and lift their lines temporarily so that the seals move to another boat (Wickens, 1994).

The use of gaffs, knives, harpoons and stones can cause severe injury to seals. At least some of the injured seals would subsequently die.

General attitude of fishermen towards seals

Although many fishermen in the Eastern Cape harbour a strong antipathy towards seals, less than 50% of skippers thought that seals should be managed (culled) to prevent negative interactions with the fishing community.

The hake longliners at Plettenberg Bay appealed for immediate action, stating that culling (or localised removal of specific animals) would help resolve the seal problem in their area.

CONCLUSION

On the Eastern Cape coast, seals break lines/tackle, take fish from the lines, cause fish schools to scatter, and reduce potential catch by feeding on fish schools near the lines. These interactions causes some financial loss to fishermen. Some fishermen deliberately kill seals in order to reduce their perceived impact. More than 1 000 are shot in this area each year. Therefore interactions are detrimental to both parties. Although individual fishermen may experience considerable disruption to their operations at times, in terms of the value of the industry as a whole, such losses are negligible .

In order to reduce the losses incurred by fisheries, and prevent shooting of seals, research is needed to develop effective non-lethal methods of deterring seals from fishing operations. Considering that 1 or 2 seals can cause losses for fishermen, culling is unlikely to reduce the magnitude of losses appreciably (Wickens, 1994). Localised removal of specific animals may be a short term solution in some areas; however, long term solutions are required. Non-lethal methods of deterring seals from operations would alleviate problems to both parties, e.g., deterrents to repel seals from fishing gear and/or conditioning seals to avoid fishing areas. The market could subsidise such research by increasing the price of fish. The closure of certain areas to fishermen should also be considered. Large numbers of seals are being shot in this area, therefore ongoing monitoring of the seal population is required.

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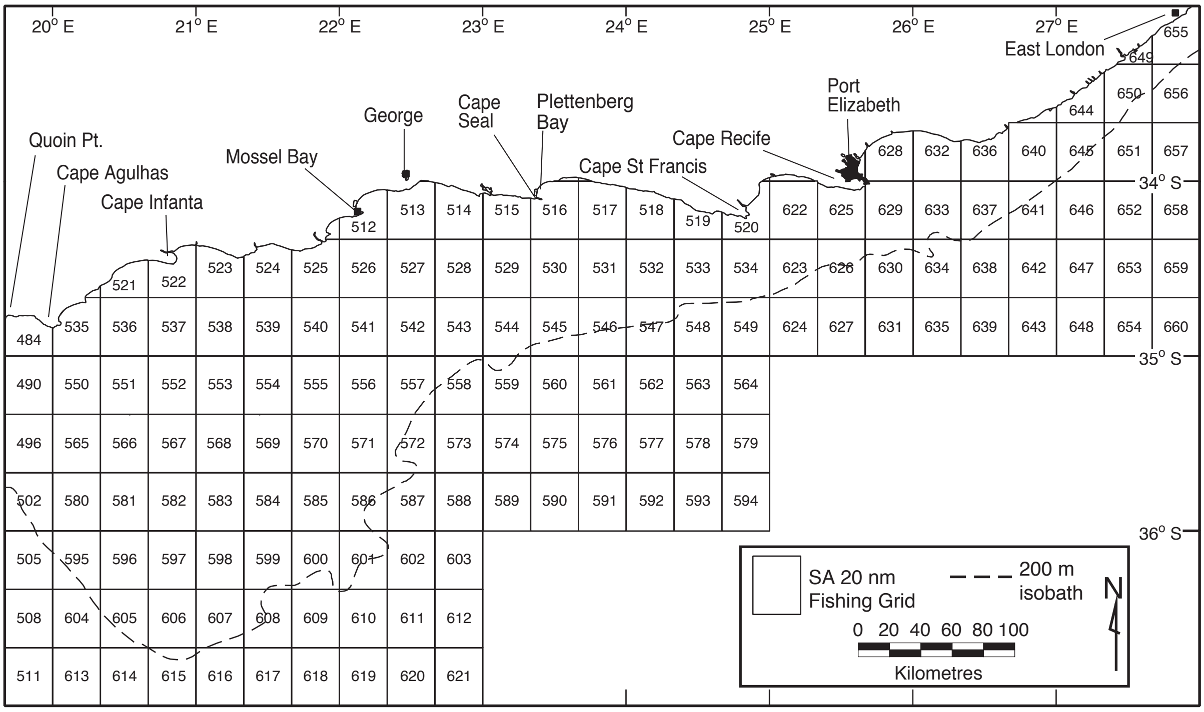
Appendix 11(b).1 *Demersal grid chart of the south and east coasts of South Africa*



Appendix 11(b).2 *Main fishing locations and the number of skippers operating in each location (n = 33 squid jig skippers)*

Fishing location[1]	Count	Percent	Fishing	Count	Percent	Fishing	Count	Percent
512*	2	0.7	533	4	1.4	623	2	0.7
513*	3	1.1	534	4	1.4	625	13	4.7
514*	3	1.1	535*	4	1.4	626	2	0.7
515	4	1.4	536*	3	1.1	628	13	4.7
516	13	4.7	537*	2	0.7	629	9	3.2
517	8	2.9	538*	2	0.7	632	12	4.3
518	12	4.3	539*	2	0.7	633	2	0.7
519	15	5.4	540*	2	0.7	636	15	5.4
520	15	5.4	541*	2	0.7	637	4	1.5
521*	2	0.7	542*	2	0.7	640	18	6.5
522*	2	0.7	543*	1	0.4	641	3	1.1
523*	2	0.7	544	1	0.4	644	14	5.0
524*	2	0.7	550*	2	0.7	645	5	1.8
525*	4	1.4	551*	1	0.4	649	1	0.4
526*	2	0.7	552*	1	0.4	650	3	1.1
527*	1	0.4	565*	1	0.4	655	3	1.1
528*	2	0.7	566*	1	0.4	661	1	0.4
529	3	1.1	567*	1	0.4	665	1	0.4
530	3	1.1	580*	1	0.4	666	1	0.4
531	3	1.1	595*	1	0.4	671	1	0.4
532	4	1.4	622	12	4.3			
	105	**37.8**		**50**	**18.1**		**123**	**44.5**

[1] Fishing locations were recorded as a grid number (see Appendix 11(b).1).

* Several of the Eastern Cape skippers also fished as far west as Cape Agulhas Point

Appendix 11(b).3 ***Main fishing locations for the 12 species of line fish listed in Table 1(b).11.*** **Fishing grid number followed by the number of skippers operating in each location (*n* = 15 skippers).**

Line fish species																							
1		**2**		**3**		**4**		**5**		**6**		**7**		**8**		**9**		**10**		**11**		**12**	
515	1	626	1	625	2	625	1	626	1	625	1	628	1	625	1	625	1	628	1	529	1	626	1
516	4	629	2	626	1	626	1	627	3	628	1	632	2			626	1			530	1		
517	1	630	1	627	1	627	1	628	1	632	1					627	1			531	1		
518	1	632	1	628	3	628	2	629	1							628	1						
625	4	633	2	629	1	629	2	630	1							629	1						
626	2	NR	2	632	1	633	1																
627	1			633	1	NR	1																
628	2			NR	1																		
629	2			NR																			
630	2																						
633	1																						
634	1																						
NR	2																						
Total	**24**		**9**		**11**		**9**		**7**		**3**		**3**		**1**		**5**		**1**		**3**		**1**

[1] Fishing locations were recorded as a grid number (see Appendix 11(b).1).

NR, grid numbers not recorded for that species.

Species codes: 1. stock fish (hake); 2.carpenter (silverfish); 3. true kob (kabeljou); 4. geelbek; 5. tuna; 6. santer; 7. dageraad; 8. roman; 9. panga; 10. elf (shad); 11. kingklip; and 12. dikbek (barred thick-lip).

Appendix 11(b). 4 ***Cape fur seals deliberately killed by fishermen along the Eastern Cape coast January 1992 to December 1995***

Acession no.	**Date**	**Approximate location**	**Sex**	**Length (SBL cm)**	**Weight (kg)**	**Cause of death**
PEM1877	2 Apr 1992	Lauries Park, PE 34°02’S, 25°23’E	M	185	68	Bullet wound between the sholders
PEM1882	6 May 1992	King’s Beach, PE 33°58’S, 25°39’E	M	180	124	Bullet wound to the stomach (rifle)
PEM2018	25 Jan 1993	Bird Island 33°51’S, 26°17’E	M	155	–	Two bullet wounds to the shoulder and neck
PEM2045	30 May 1993	Schoenmakerskop 34°02’S, 25°32’E	M	145	–	Bullet wound to the stomach
PEM2050	8 Jun 1993	Plettenberg Bay 34°07’S, 23°25’E	M	165	–	Bullet wound[1]
PEM2134	28 Dec 1993	Noordhoek 34°02’S, 25°39’E	M	216	–	Bullet wound to the stomach
PEM2143	28 Jan 1994	Seaview 34°01’S, 25°17’E	M	189	114	Two bullet wounds to the head
PEM2198	Jul 1994[3]	Plettenberg Bay 34°03’S, 23°24’E	M	105	28	Blow to the head[2] (severe hemorrhage extending from the nasal to the mid orbit)
PEM2203[4]	18 Jul 1994	PE Harbour 33°58’S, 25°37’E	M	240	134	Stonned and gaffed
PEM2406	25 Jul 1995	Swartkops River	M	154	72	Bullet wound to the shoulder and lungs (one shot gun pellet retrieved)
PEM2411	24 Aug 1995	Plettenberg Bay	M	155	85	Bullet wound to lower jaw; punctured eye; pellet scars on fore flippers (shot gun pellet retrieved)

[1] Examined by Cape Nature Conservation Ranger (confirmation of bullet wound).

[2] Possible interaction with a vessel, but more likely to have been hit with a stone or club.

[3] Autopsy performed 6 Jul 1994; dead animal stored in freezer at Plettenberg Bay.

[4] Fishermen observed throwing stones at the seal; gaff wound to the lower lip and pellet; and severe lacerations over the eye (eye pushed downward into the socket).

CHAPTER 11(c)

Operational interactions between Cape fur seals *Arctocephalus pusillus pusillus* and fisheries off the Eastern Cape coast of South Africa: part three, entanglement in man-made debris

INTRODUCTION

Entanglement in man-made debris lost or discarded from fishing vessels is a contributing factor to the decline of *Callorhinus ursinus*, northern fur seals (Flower, 1985, 1987; Stewart & Yochem, 1987), and is a potential threat to other species of fur seals, including *Arctocephalus pusillus doriferus*, Australian fur seal (Pemberton *et. al.,* 1992; Prendergast & Johnson, 1996) and *Arctocephalus gazella*, Antarctic fur seals (Croxall *et. al.,* 1990). Much of the debris discarded and lost by fishing vessels is not biodegradable and therefore remains at sea for a long time. Furthermore, much of the debris floats and therefore has the potential to entrap seals swimming at sea. Seals may become entangled when playing with the debris; trying to remove entangled fish from the debris; or attempting to haul-out and rest on the debris (Laist, 1987). Many entangled animals subsequently die.

The Cape (South African) fur seal, *Arctocephalus pusillus pusillus*, occurs only on the coasts of South Africa and Namibia, and is the only resident seal species in southern Africa. Breeding rookeries are distributed from Black Rocks (33º 50'S, 26º16'E) in Algoa Bay, on the south east coast of Southern African, to Cape Cross (21º 46'S, 13º 58'E) in Namibia. The majority of seals occur on the west coast. The remainder of the population (*c.* 8.5%; 140 000 seals in 1993), inhabits the south/east coast, between False Bay and Algoa Bay, at five breeding colonies and one haul-out site (J.H.M. David, pers. comm.). Their distribution overlaps important commercial fishing grounds. Therefore, Cape fur seals are occasionally seen with man-made objects around their necks, predominantly mono-filament line and string made of synthetic fibre. Other objects include fishing net, plastic straps, rubber O-rings and wire (Shaughnessy, 1980).

In recent years, fishing effort in Eastern Cape waters (Plettenberg Bay, 33º07'S, 23º25'E, to the Kwazulu-Natal border, 31º05'S, 30º11'E) has increased significantly. This has resulted in an increase in lost or discarded trawl nets and trawl net fragments, ropes and lines. In the trawl fishing industry, commercial bottom trawl skippers are likely to lose or damage nets as they extend their fishing grounds. Fragments of net float to the surface or remain on the sea bed depending on the net material. An estimated 2–3 sets of gear are lost per year by the inshore trawl fleet (Peter Sims, pers. comm.). Longline fishermen frequently lose 100s of meters of rope, especially off Cape St Francis where the currents are strong and fast moving (Peter Sims, pers. comm.). The effect of this on the local seal population is not know.

The present study documents the incidence and nature of entanglement of Cape fur seals off the Eastern Cape coast of South Africa.

METHODS

Data was collected from three sources: (i) observations at Black Rocks seal colony, Algoa Bay and Rondeklippe haul-out site, Plettenberg Bay; (ii) examination of stranded (dead) seals; and (iii) examination of seals brought into the Port Elizabeth Oceanarium (PEO) for rehabilitation.

Between 10 March 1993 and 20 January 1995, seven day trips were made to Black Rocks to assess the number of seals entangled in man-made debris. Counts began at 0800 hrs from an inflatable boat, *c.* 10 m from the colony, and were completed on foot.

Between January 1991 and August 1996, seals beached (dead) or injured along the coast were examined for signs of entanglement. In addition, old Port Elizabeth Museum (PEM) stranding forms and PEO log books (1987–1991) were examined for records of entangled seals.

Where possible, the following information was recorded: date of observation; location; sex; age group of entangled animal; the type of object the animal was entangled in; and the position of the object on the body of the seal. Entangled animals were classified as pups; juveniles (7 months to 2 years) and subadults/adults (≥ 3 years of age).

To determine the percentage of entangled animals at the two seal colonies, ground counts of entangled seals were conducted during the breeding season, when the number of animals was maximal. These took place at Black Rocks on 16 November 1993 and 20 December 1993; and at Rondeklippe on 5 December 1994. The total number of seals at Black Rocks was estimated from near vertical aerial photographs taken on 24 December 1993 following Stewardson (1999).

RESULTS

Black Rocks seal colony

During the seven day trips to Black Rocks seal colony, a total of 10 entangled seals was observed (Table 11(c).1). Four animals were entangled in mono-filament line, five in rope, and one in unidentified material which had embedded deep into the neck of the animal. Juveniles accounted for 30% of entanglements and subadult/adults accounted for 70%. The ratio of entangled females to entangled males was 1 : 8.

In addition, at least three seal pups entangled in a section of discarded trawl net were reported near Black Rocks on 28 December 1992 by the skipper of *Sea Princess*, Mr D. Rodocanachi. It is probable that the young pups (*c.* 4 weeks of age) become entrapped in the net while playing, and were then carried away

Fig. 11(c).1 Cape fur seals trapped in the factory area of commercial trawl vessels are often killed, secured with rope, hauled up onto the deck, and thrown over board. Dead animals which enter the factory area with the catch are also removed in this way (photo: C. Urquhart).

Fig. 11(c).2 Cape fur seals entangled in a trawl net fragment hauls-out at Port Elizabeth Harbour (photo: Eastern Province Herald).

from the colony as the net drifted with the current. Wind speed was 10 knots in a W-SW direction. Swell height was 0.5 m.

Stranded (dead) seals

From January 1991 to December 1995, a total of 77 Cape fur seals were found beached (dead) along the Eastern Cape coast. Only one of these animals (1.30%) was entangled in man-made debris (PEM2351).

Examination of old stranding records (1987 to 1991) indicated that at least three seals had died because of entanglement in man-made debris. Two animals were entangled in trawl net fragments and one in rope. One of these animals (PEM1644) was observed alive *c.* 2 week prior to the stranding with the net fragment entangled around its neck.

Stranded seals 'tied in rope'

Occasionally stranded seals 'tied in rope' wash ashore along the Eastern Cape coast. These animals become trapped in the factory area of a commercial trawl vessel and are subsequently killed (if not already dead). They are secured with rope, hauled up on deck, and then thrown overboard.

From 1992 to 1995, three seals 'tied in rope' were observed along the Eastern Cape coast:

On 8 November 1995 the carcass of one adult male (PEM2454), 196 cm in length, was found at Noordhoek (34°02’, 25°39’) with rope tied around its girth.

In 1992/1993, the carcasses of two large adult males with rope around their neck and girth were photographed by a newspaper photographer (Fig. 11(c).1). The exact details were not reported.

These three animals have been excluded from analysis.

Live Cape fur seals treated at the Port Elizabeth Oceanarium

From January 1987 to September 1991, a minimum of eight entangled Cape fur seals were treated at the Port Elizabeth Oceanarium (Table 11(c).1). Two animals were entangled in mono-filament line, three in trawl net fragment (Fig. 11(c).2), and three in rope.

Table 11(c).1 *Cape fur seals entangled in man-made debris off the Eastern Cape coast of South Africa*

	Date	Location	Sex	Age group	Mono-filament line	Trawl net	Rope	Position of object	Other comments
Observations at seal colonies									
1	28 Dec 1992	Black Rocks	–	Pup		*[1]		Body	
2	28 Dec 1992	Black Rocks	–	Pup		*[1]		Body	
3	28 Dec 1992	Black Rocks	–	Pup		*[1]		Body	
4	10 Mar 1993	Black Rocks	–	S/A	*			Neck	Line cutting through skin
5	16 Nov 1993	Black Rocks	M	S/A	–	–	–	Neck	Wound too deep to identify the type of material
6	20 Dec 1993	Black Rocks	M	S/A	*			Neck	Line cutting through skin
7	20 Dec 1993	Black Rocks	M	S/A			*	Neck	
8	20 Jan 1994	Black Rocks	F	S/A	*			Neck	Line cutting through skin
9	22 Mar 1994	Black Rocks	M	S/A			*	Neck	Line cutting through skin
10	15 Sep 1994	Black Rocks	M	Juv			*	Neck	Line cutting through skin
11	15 Sep 1994	Black Rocks	M	Juv			*	Neck	Line cutting through skin
12	15 Sep 1994	Black Rocks	M	Juv			*	Neck	Line cutting through skin
13	20 Jan 1995	Black Rocks	M	S/A	*			Neck	Line cutting through skin
14	5 Dec 1994	Rondeklippe	M	S/A	*[2]			Neck	120 pound fishing line cutting into the muscle (deep wound)
15	2 Dec 1994	Rondeklippe	F	–		*[3]		Body	PEM2351; SBL 113 cm; body mass 23 kg
Stranded (dead) seals									
16	7 Nov 1987	Jeffreys Bay (34°03’S, 24°55’E)	F	A			*	Neck	PEM1478; SBL 164 cm; body mass 48 kg
17	16 Sep 1989	Seaview (34°01’S, 25°17’E)	_	S/A		*		Neck	PEM1644; SBL 136 cm
18	4 Oct 1989	Seaview (34°01’S, 25°17’E)	_	S/A		*		Body	PEM1647; SBL 127 cm; very thin
Live seals rehabilitated at the Port Elizabeth Oceanarium									
19	1 Dec 1987	Bushy Park	M	Juv		*		Neck	± 2 y of age
20	13 Jan 1988	–	–	S/A		*		Body	
21	24 Jun 1988	–	M	S/A			*	Neck	Rope cutting through skin
22	31 Dec 1988	–	M	S/A		*		Body	Mesh cutting into muscle (deep wounds)
23	10 Jul 1990	–	–	–	*			Neck	Line cutting through skin[4]
24	29 Dec 1990	Port Elizabeth Harbour (33°58’S, 25°37’E)	–	–			*	Neck	
25	10 Aug 1994	King’s Beach (33°58’S, 25°39’E)	M	Pup	*			Neck	Line cutting into muscle (deep wound & infection)
26	10 Oct 1994	Port Elizabeth Harbour (33°58’S, 25°37’E)	–	–			*	Neck	Line cutting through skin
26					**7**	**9**	**9**		

[1] All three pups were entangled in the same piece of trawl net. The entangled pups were drifting away from Black Rocks.

[2] Possibly snoek line (seals at Rondeklippe regularly frequent the ‘snoek patch’) or longline.

[3] The trawl mesh measured 270 cm in length and 160 cm in width.

[4] Seal had been gaffed by fishermen.

PEM, Port Elizabeth Museum accession number.

SBL, standard body length (straight line from tip of snout to tip of tail with the animal lying on its back).

Incidence of entanglement at Black Rocks

The total population estimate for the 1993 breeding season at Black Rocks was 915 animals (i.e., 183 pups counted from aerial photographs). One entangled seal was observed on 16 November 1993, and two entangled seals were observed on 20 December 1993. Therefore, the minimum estimated frequency of entanglement for the Black Rocks colony in 1993 was *c.* 0.11–0.22%. During the seven field trips to Black Rocks, a mean of 1.4 entangled seals was observed per trip.

Incidence of entanglement at Rondeklippe

The total population estimate for the 1994 breeding season at Rondeklippe was 11 animals (small haul-out site). One entangled seal was observed on 2 December 1994, and a second entangled animal was observed on 5 December 1994. This suggested that even though there are a small number of seals using this haul-out site, the frequency of entanglement was high.

One of the animals was a female (PEM2351) entangled in a triangular piece of trawl net which measured 270 cm in length and 160 cm in width. She was observed alive on 2 December 1994 but died five days later. The second animal was an old male with 120^{+} pound fishing line looped twice around its neck. The line was probably used by longline or snoek fishermen.

DISCUSSION

Type of objects

A total of 26 Cape fur seals entangled in man-made debris were recorded along the Eastern Cape coast of South Africa (Table 11(a). 1). Mono-filament line accounted for 28% of entanglements; trawl net fragments accounted for 36%, and rope accounted for 36%. One object, a neck collar embedded deep into the flesh, was not identified. Other objects such as straps, rubber O–rings and wire reported by Shaughnessy (1980) were not observed in the present study.

Off the Eastern Cape coast, the bottom trawl fishery use 110 mm stretched mesh for the hake fishery, and 85 mm for the horse mackerel fishery. This is made of polyethylene with nylon codends. Seals become entangled in this material when whole nets are lost; pieces of damaged net break off or are discarded; or when entrapped seals tear free from the nets. As trawlers extend their fishing grounds they are likely to loose/damage gear.

The moni-filament lines are likely to be from the squid, longlining and teleost-handline fisheries. Hake longliners are active south of Plettenberg Bay, whereas squid jig fishermen mainly operate eastwards of Plettenberg Bay to Algoa Bay. When seals take fish/squid directly from fishing lines they can become entangled. They also can become entangled in lost or discarded fishing line floating at the water surface.

Ropes come from numerous sources, especially the longlining sectors. Hundred's of meters of rope are lost regularly by longliners, especially near Cape St Francis where bottom currents are strong. The ropes entangle and drift westwards onto the central Agulhas Bank (Peter Sims. pers. comm.).

Entangled fishing line was located at Black Rocks on three separate occasions. A narrow piece of trawl net *c.* 2.5 m in length was also observed. It is not clear if these objects were washed up onto Black Rocks; or carried their by seals who managed to dislodge themselves from the material.

Age class of entangled animals

Of the 22 animals for which age class was recorded, pups accounted for 18.2% (n = 4) of entanglements, juveniles accounted for 18.2% (n = 4), and subadult/adults accounted for 63.6% (n = 14). Possibly reasons why older animals are more likely to become entangled than younger animals are: (i) older animals have learnt to associate fishing vessels with food and are therefore more likely to take fish from lines/nets; and (ii) older animals travel further distances than young animals and therefore have a greater probability of encountering floating debris.

Sex ratio of entangled animals

Of the 20 animals for which sex was recorded, 13 were males and seven were females (1 female : 1.86 males). Possibly reasons why more males than females become entangled in marine debris are: (i) males are more likely to travel further from the rookery and therefore have a greater probability of encountering floating debris than females; and (ii) males may be more likely to approach fishing vessels and take fish from lines.

Incidence of entanglement

The minimum estimated frequency of entanglement for Cape fur seals at the Black Rocks colony in 1993 was *c.* 0.11–0.22% (present study). The incidence of entanglement among other species of fur seals is: 1.9% for the Australian fur seal in Tasmanian waters (Pemberton *et. al.,* 1992); 0.4% for the northern fur seals (Fowler, 1987), and 0.4–1.0% for Antarctic fur seals (Croxall *et. al.,* 1990). Therefore, the incidence of entanglement for Cape fur seals is comparatively low. Shaughnessy (1980) reported that the incidence of entanglement of immature Cape fur seals on the south and west coast of South Africa was 0.11–0.66% (Shaughnesy, 1980). Estimates for Black Rocks are towards the lower end of this range (present study).

Fate of entangled seals

The majority of objects (73%) were neck collars. These collars are made of highly durable materials. As the animal grows, the neck collar tightens, and cuts through the skin, into the muscle. If the collar does not fall off the animal, pressure on the oesophagus and trachea may impede feeding and respiration. The animal may subsequently die of starvation or strangulation. Furthermore the open wound may become infected, and the animal may subsequently die of septicemia. In the present study, 11 collars had cut into the skin of the animal, and three had penetrated the muscle. The neck wound of one animal was infected.

Entanglement in trawl fragments impedes general movement, travel and foraging ability. The entangled animal is also at risk of drowning and is more vulnerable to predation. Feldkamp *et. al.,* (1989) found that net fragments over 200 g can elevate the energetic cost of travel of northern fur seals. In order to maintain body condition, daily food intake must therefore be increased. Entangled animals unable to consume sufficient food soon become weak and die. Lactating females may be unable to produce sufficient milk. Their pups may subsequently starve.

CONCLUSION

Cape fur seals off the Eastern Cape coast are occasionally entangled in man-made debris, e.g., trawl nets, mono-filament line and rope. Depending on the type of material, the entangled animal may suffer physical injury, develop septicemia, died of strangulation, die of starvation, or drown.

Although debris-related mortality does not appear to impact significantly on the local seal population, much of the materials which entangles seals is highly durable, and floats at the water surface for long periods. Such material is likely to accumulate in areas of up- or down- welling where the animals feed, e.g., regular surveys of the 43 mile Mosgas pipeline (central Agulhas Bank) using video cameras frequently shows tangles of rope and sections of netting (Peter Sims, pers. comm.). As the fishing industry continues to expand, more synthetic material will accumulate, and the incidence of entanglement in this area will subsequently increase. Therefore continued monitoring of the population, and the nature of entanglement, is essential.

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CHAPTER 12

Concentrations of heavy metals (Cd, Cu, Pb, Ni & Zn) and organochlorine contaminants (PCBs, DDT, DDE & DDD) in the blubber of Cape fur seals *Arctocephalus pusillus pusillus* off the Eastern Cape coast of South Africa

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ABSTRACT

The concentration of heavy metals (Cd, Cu, Pb, Ni and Zn) and organochlorine contaminants (PCBs, DDT, DDE and DDD) in the blubber of 12 adult male Cape fur seals, *Arctocephalus pusillus pusillus*, inadvertently caught in trawl nets off the Eastern Cape coast of South Africa during commercial fishing operations between May 1993 and October 1994, was investigated. The median and range of concentrations for each metal were, in µg/g wet weight: Cd, 0.4 (<0.04–0.53); Cu, 2.6 (2.17–7.43); Pb, 0.7 (0.54–0.99); Ni, 17.7 (9.39–23.18) and Zn, 11.5 (3.14–16.65). Dry weights were: Cd, 0.5 (<0.04–0.59); Cu, 2.9 (2.47–8.45); Pb, 0.6 (0.54–1.14); Ni, 17.0 (10.79–28.22) and Zn, 12.8 (3.61–20.26). Concentrations of Cd, Pb and Zn were in the limits of reported values; however Cu and Ni levels were considerably higher. There is no evidence that the elevated levels of Cu and Ni reported in this study would pose a serious threat to the health of individual animals; however, high concentrations of these metals may be sufficient to result in some additional stress to animals when they mobilise their lipid reserves during illness or starvation. Nickel and Cd concentrations appeared to increase with age; however, small sample size prevented statistical analysis. Concentrations of organochlorines (µg/g wet weight) were below the limit of detection.

INTRODUCTION

Organochlorine contaminants, particularly polychlorinated biphenyls (PCBs) and the DDT group of insecticides are persistent environmental contaminants. These lipophilic compounds are known to accumulate in the fatty tissue of pinnipeds and other marine mammals (Risebrough, 1978). Pinnipeds are ideal repositories for high concentrations of organochlorines because they are long lived top predators which have large fat reserves in relation to their body size (Holden, 1972, 1978). In wild pinniped populations, the detrimental effects of organochlorines are difficult to establish; evidence is mostly circumstantial. However, high concentrations of certain organochlorines have been associated with premature births in California sea lions, *Zalophus californianus* (DeLong *et al.*, 1973); decreased reproductive rates and reproductive abnormalities in harbour seals, *Phoca vitulina* (Duinker *et al.*, 1979; Reijnders, 1980, 1982, 1986); suppression of natural killer cell activity in harbour seals (Ross *et al.*, 1997); and pathological changes of bony tissue and reproductive organs in Baltic grey seals, *Halichoerus grypus,* and ringed seals, *Phoca hispida* (Helle *et al.*, 1976; Olsson 1978; Bergman & Olsson, 1986, 1989; Bergman *et al.*, 1986, 1992; Olsson *et al.*, 1994).

Other pollutants which pose a potential threat to the future status of pinniped populations are the heavy metals. High concentrations of certain metals are a potential source of clinical disease and stress in marine mammals (Eisler, 1981; Wagemann & Muir, 1984; Thompson 1990; Skoch, 1990; Olsson *et al.*, 1992; Law, 1996). Of the metals which are considered to be toxic, Hg, Pb and Cd are thought to represent the greatest health risk to pinnipeds (Thompson, 1990). The toxic effects of these metals have been summarised by Skoch (1990).

The Cape fur seal, *Arctocephalus pusillus pusillus,* is the only indigenous breeding pinniped in southern Africa. It breeds at 25 colonies from Black Rocks (lat. 33° 50’S, long. 26° 15’E) on the south-east coast of South Africa, to Cape Cross (lat. 21° 46’S, long. 13° 57’E), Namibia. Current population size is estimated to be 1.5 to 2 million (Butterworth & Wickens, 1990). On the south-east coast, where two breeding colonies occur (Seal Island, Mossel Bay; Black Rocks, Algoa Bay), population levels are declining (SFRI, unpubl. data; Stewardson, unpubl. data), underlying the immediate need to document the biology of these top predators and evaluate potential threats.

DDT, dieldrin and PCBs have been used extensively in South Africa primarily as insecticides, fire retardants or heat absorbents; however, few studies have examined the occurrence of chlorinated hydrocarbon residues in the resident seal population (Henry, unpubl. report; Cockcroft & Ross, 1991). Furthermore, industrial development along the coast of southern Africa has resulted in an increase in the presence of toxic metals in the marine environment, particularly in inshore waters (Allan Connell, pers. comm.). The effects of industrialisation on the health of resident pinnipeds is not known.

Here we investigate the concentrations of heavy metals (Cd, Cu, Pb, Ni and Zn) and organochlorine contaminants (PCBs, DDT, DDE and DDD) in the blubber of 12 healthy adult male Cape fur seals from the Eastern Cape coast of South Africa. The results are compared with concentration ranges reported in the literature for other species of pinnipeds, and the toxic significance of these concentrations discussed. Age accumulation effects are also considered.

MATERIALS AND METHODS

Collection of samples

Twelve adult male Cape fur seals were included in this study (Table 12.1). These animals were inadvertently drowned within trawl nets during commercial fishing operations off the Eastern Cape coast (Fig. 12.1), between May 1993 and October 1994. Routine necropsies were performed on the fresh carcasses and biological parameters recorded based on recommendations of the Committee on Marine Mammals, American Society of Mammologists (1967). Blubber thickness was used as an index of physical condition. Specimens were examined for gross abnormalities (histopathological studies were not conducted). Blubber samples of approximately 20 g were removed from the anterior end of the sternum, wrapped in aluminium foil and stored at –20˚C for subsequent analysis. Upper canines were collected for aging purposes following Oosthuizen (1997), assuming a birth date of December 1 (Shaughnessy & Best, unpubl. report).

Gas chromatography

Thawed samples of blubber (15 g) were mixed with anhydrous sodium sulphate and subject to soxhlet extraction with hexane for 4 h. Fat extract (0.3–0.4 g) was cleaned up using alumina and silica gel as adsorbents. Concentrations of polychlorinated biphenyls (PCBs-57 in total) and DDT and its metabolites (DDE and DDD), were estimated using high resolution capillary gas chromatography equipped with a 30 m fused silica column (0.32 mm i.d.), coated with SPB5 as a liquid phase (0.22 mm) and ^{63}Ni electron capture detection (ECD). The detector temperature was 320˚C. The oven was programmed at a rate of 10˚C. min^{-1} from 50˚C to 180˚C (1 min), and then at 2˚C. min^{-1} to 220˚C, and at 4˚C. min^{-1} to 260˚C. The limits of detection of the residues represent amounts giving at least 2.5% full scale detection on the chart reader. The limits were DDE 0.5 pg/µl; DDD 0.5 pg/µl; DDT 0.75 pg/µl. Detection limits for a 10 g sample with a fat content of 0.5% was 500 pg/g for the PCBs. Full details of procedures are given in de Kock (1990).

The chlorinated hydrocarbon concentrations were determined by comparing the peak characteristics and retention times obtained from the samples with those of calibration range of standards injected daily. Compounds were quantified with standards obtained from the National Research

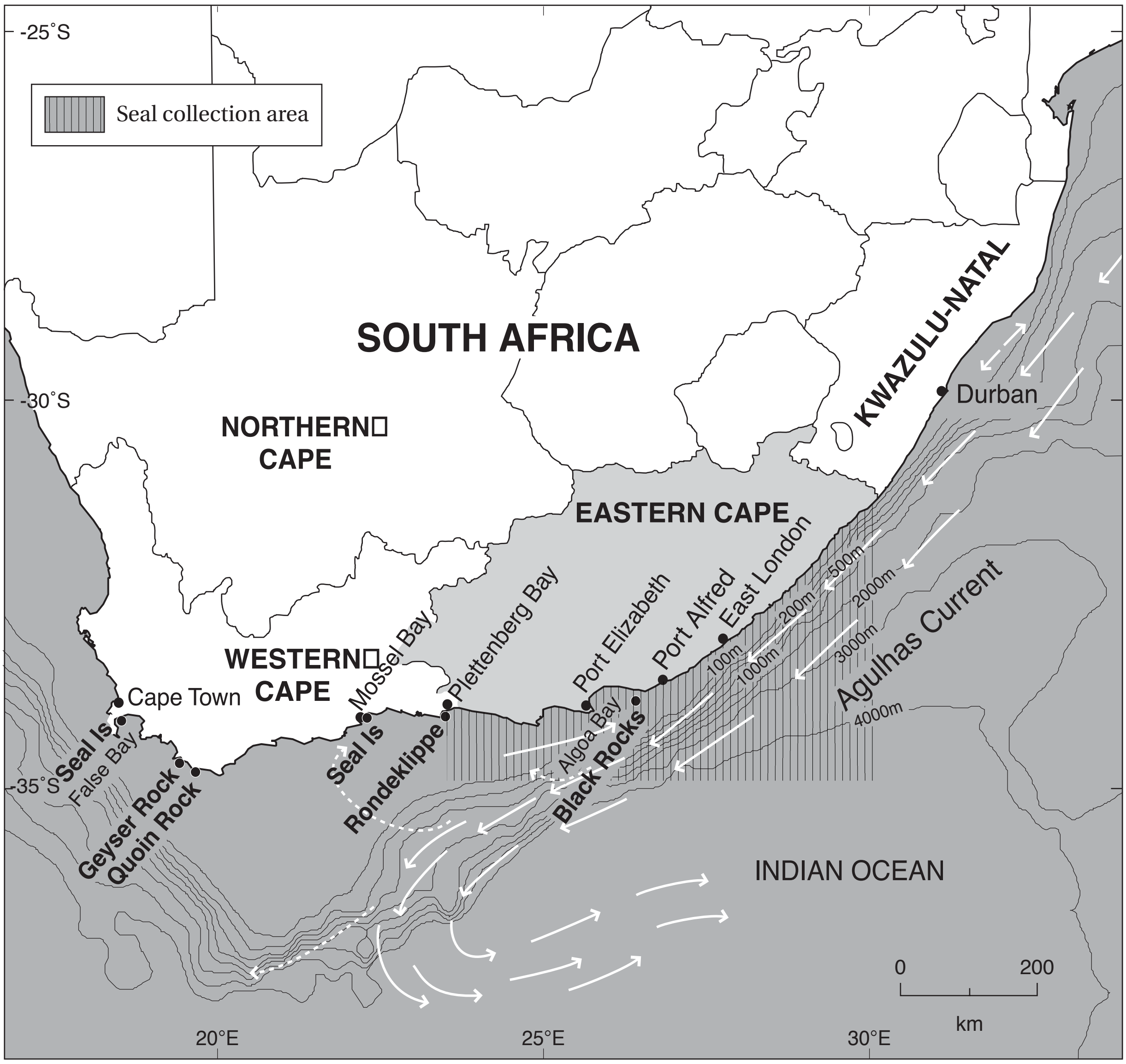

Fig.12.1 The breeding range of Cape fur seals along the south coast of southern Africa.
Seals ($n = 12$) were collected from the Eastern Cape coast.

Council, Marine Analytical Chemistry Standards Program (MACSP).

Atomic absorption spectroscopy

Thawed samples of blubber (2.5–3.0 g) were dried at 90˚C for 24 h, cooled in a desiccator, brought to room temperature and weighed to obtain dry weight. The dried samples were digested with concentrated nitric acid and the sediments with a 4:1 mixture of nitric and perchloric acids. Concentrations of Cd, Cu, Pb, Ni and Zn were determined by atomic absorption spectroscopy (single-element hollow cathode lamp and a deuterium lamp background corrector). The limits of detection for each metal were Cd, 2 µg/l (10 µg/l); Cu, 3 µg/l (30 µg/l); Pb, 10 µg/l (100 µg/l); Ni, 10 µg/l (70 µg/l) and Zn, 1 µg/l (8 µg/l). Suggested working concentrations are given in parentheses. Full details of procedures are given in Watling (1981). Compounds were quantified using MERK standards.

Concentrations are expressed as µg/g wet weight and µg/g dry weight. The median and range were used rather than the mean and standard deviation because the data are skewed and there are extreme data whose exact values are unknown (T. Prvan, pers. comm.). In pinnipeds, Cd, Cu and Zn concentrations tend to decrease in the order kidney/liver > muscle/blubber (Thompson, 1990). Therefore, we compare the results of the present study with concentrations from the blubber/muscle tissue of other pinnipeds.

RESULTS AND DISCUSSION

Details of the 12 male specimens are presented in Table 12.1. Animals were in good physical condition with an average blubber thickness of 29 ± 8 mm. Apart from high parasite burdens in some animals (Stewardson & Fourie, 1998), post-mortem examination showed no gross abnormalities.

Table 12.1 *Details of 12 adult male Cape fur seals caught inadvertently within trawl nets during commercial fishing operations off the Eastern Cape coast of South Africa between May 1993 and October 1994*

Accession no.[a]	Date of collection	Age (yrs)	Body length (cm)	Girth (cm)	Blubber thickness[b] (mm)
2047	20 May 1993	7	167	106	24
2048	20 May 1993	8	157	95	18
2053	28 June 1993	7	153	103	25
2055	29 June 1993	8	179	122	27
2056	29 June 1993	8	139	92	27
2252	22 August 1994	9	172	122	26
2253	27 August 1994	NR	152	97	33
2254	27 August 1994	NR	146	95	33
2256	17 September 1994	NR	198	144	45
2257A	19 September 1994	6	142	93	17
2257B	7 October 1994	9	170	120	40
2258	8 October 1994	8	186	131	30

[a] Port Elizabeth Museum, seal accession number.
[b] Blubber thickness taken at the base of the sternum (index of physical condition).
NR, not recorded.

Cadmium (Cd), lead (Pb) and zinc (Zn)

Concentrations of Cd (0.4 wet wt.), Pb (0.7 wet wt.) and Zn (11.5 wet wt.) were in the limits of reported values for the blubber and muscles of other pinnipeds (Table 12.2, 12.3). However, seven seals showed Cd concentrations towards the upper limits of this range. It is thought that diet plays an important role in determining Cd concentrations in pinnipeds, with those species that feed predominantly on cephalopods or euphausiids showing higher concentrations of Cd than those that feed on fish (Hamanaka & Mishima, 1981; McClurg, 1984; Pena *et al.*, 1988; Thompson, 1990). Considering that Cape fur seals feed on both cephalopods (17%) and teleost fish (75%) (David, 1987; Lipinski & David, 1990), and have a comparatively long life-span of approximately 20 years (Wickens, 1993), we would also expect to find higher Cd concentrations in these animals than in strictly fish eating species.

The highest Cd concentrations (0.5 µg/g wet wt.) were found in the two largest males (PEM2258 and PEM2256), supporting reports that Cd accumulates in pinniped tissue with increasing age (Roberts *et al.*, 1976; Drescher *et al.*, 1977; Hamanaka *et al.*, 1982; Thompson, 1990; Malcolm *et al.*, 1994). There is no evidence in the literature to suggest that Pb and Zn concentrations increase with increasing age (Roberts *et al.*, 1976; Drescher *et al.*, 1977; Helle, 1981; Hamanaka *et al.*, 1982; Goldblatt & Anthony, 1983; Honda & Tatsukawa, 1983; Wagemann *et al.*, 1988).

Copper (Cu)

Copper concentrations in the blubber of Cape fur seals ranged from 2.17–3.21 µg/g wet wt., and 2.47–4.17 µg/g dry wt., with the exception of one animal (PEM2055) that had a very high concentration of 7.44 µg/g wet wt. and 8.45 µg/g dry wt. (Table 12.2). Most of these concentrations were outside the range of reported values for the blubber and muscle of other pinnipeds (Table 12.3).

Copper is an essential element and is therefore presumably under close physiological regulation (Thompson, 1990). In humans, high concentrations of Cu (above 50 µg/g body weight) can cause cirrhosis of the liver and, in extreme cases, death (NHMRC/ARMCANZ, 1996). Localised anthropogenic sources of Cu may result in deleterious effects to marine life (Thompson, 1990).

As with Cd, diet is thought to play an important role in determining Cu concentrations in seals, with those species that feed predominantly on cephalopods having higher levels of Cu than fish-eating species (McClurg, 1984). High levels of Cu found in the present study presumably reflect the relatively high levels of metal in squid. Copper concentrations in marine vertebrates do not appear to have a geographical bases (Thompson, 1990).

Table 12.2 ***Heavy metal concentrations in the blubber of 12 adult male Cape fur seals from the Eastern Cape coast, South Africa.*** **Concentrations of metals are given in µg/g wet wt. and µg/g dry wt.**

Accession	**Cd**		**Cu**		**Pb**		**Ni**		**Zn**	
no.[a]	**wet**	**dry**	**wet**	**dry**	**wet**	**dry**	**wet**	**dry**	**wet**	**dry**
2047	<0.04	<0.04	2.17	2.49	0.54–0.81	0.54–0.81	9.39	10.79	3.14	3.61
2048	<0.04	<0.04	2.85	3.51	0.54–0.81	0.54–0.81	12.73	15.64	4.83	5.93
2053	<0.04	<0.04	3.21	4.14	0.54–0.81	0.54–0.81	11.97	15.42	6.30	7.90
2055	<0.04	<0.04	7.44	8.45	0.54–0.81	0.54–0.81	11.98	13.61	6.30	7.15
2056	<0.04	<0.04	2.78	3.23	0.54–0.81	0.54–0.81	12.03	13.97	4.81	5.59
2252	0.44	0.51	2.48	2.90	0.88	1.03	21.17	24.72	14.70	17.16
2253	0.46	0.52	2.19	2.47	0.72	0.81	16.25	18.35	12.06	13.62
2254	0.49	0.55	2.55	2.85	0.87	0.97	21.77	24.37	14.24	15.95
2256	0.50	0.57	2.36	2.70	0.99	1.14	17.74	20.29	11.62	13.30
2257A	0.42	0.46	2.60	2.88	0.71	0.79	20.26	22.45	14.09	15.62
2257B	0.42	0.52	2.75	3.35	0.93	0.11	23.18	28.22	16.65	20.26
2258	0.53	0.59	2.41	2.71	0.86	0.97	14.67	16.47	11.40	12.79
Median[b]	0.4	0.5	2.6	2.9	0.7	0.6	17.7	17.0	11.5	12.8
Range	<0.04–0.53	<0.04–0.59	2.17–7.44	2.47–8.45	0.54–0.99	0.54–1.14	9.39–23.18	10.79–28.22	3.14–16.65	3.61–20.26

[a] Port Elizabeth Museum, seal accession number.

[b] The midpoint of the interval 0–0.04 was used to calculate the median for < 0.04; the midpoint of the interval 0.54–0.81 was used to calculate the median for 0.54–0.81.

Nickel (Ni)

The range of concentrations for Ni in the blubber of Cape fur seals was 9.39–23.18 µg/g wet wt. and 10.79–28.22 µg/g wet wt. (Table 12.2). These values are unusually high considering that the concentrations of Ni in marine mammals tend to be less than 0.5 µg/g wet wt. (Thompson, 1990) (Table 12.3). Although contamination of samples with Ni during laboratory analysis should not be discarded, retesting of all samples using new equipment and chemicals did not suggest that values were inaccurate. Elevated concentrations of Ni have been recorded in the liver of Ross seals from Antarctica (4.8 µg/g dry wt.) (McClurg, 1984), and the blubber of a vagrant leopard seal, *Hydrurga leptonyx,* from South Africa (8.39 µg/g wet wt.) (Stewardson, unpubl. data).

In terrestrial mammals, high levels of Ni (over 100 µg/g body weight per day) can cause liver and kidney toxicity, alter body weights and affect the immune system (NHMRC/ARMCANZ, 1996). However, little is known of the effects of Ni toxicity in marine mammals (see Law, 1996).

On the east coast of South Africa, Ni is used in the electroplating industry, chemical marine industries and in oil refining (NHMRC/ARMCANZ, 1996), and was exported from the Port Elizabeth harbour throughout the 1900s, until 1984. Therefore, industrial activity may be a possible source of contamination. However, the origin is probably geological; Ni concentrations in bivalves from unpolluted and polluted regions of the Cape south coast are considerably higher than values considered high by the US ‘Mussel Watch’ programme (Gardner *et al.*, 1985).

For the range of values calculated in the present study, there is a suggestion that blubber Ni concentrations increase with increasing age, i.e., the highest concentrations (21.17 and 23.18 µg/g wet wt.) were found in animals 9 years of age (PEM2252 and PEM2257B).

Organochlorines

In the present study, chlorinated hydrocarbon residue concentrations in adult male Cape fur seals were below the limits of detection (Table 12.4). Although there is no baseline contaminant data for comparative purposes from healthy pinniped tissue in this area, earlier studies of beach-stranded (partially emaciated) animals from the east coast (Cockcroft & Ross, 1991), and healthy animals from the south-west Cape and Namibia (Henry, unpubl. report), suggest that pollutant levels have declined since the 1970s (Table 12.4).

Table 12.3 ***Heavy metal concentrations in the blubber and muscle of pinnipeds from different geographical locations: comparison of results of this work with values from the literature.*** **Concentrations of metals are given as the range (or mean ± SD) in µg/g wet wt.**

Species	Tissue	Cd	Cu	Pb	Ni	Zn	Area
Cape fur seal	B	<0.04–0.53	2.17–7.44	0.54–0.99	9.39–23.18	3.14–16.65	Eastern Cape$^{(1)}$
Arctocephalus p. pusillus		[12]	[12]	[12]	[12]	[12]	(South Africa)
South American fur seal	M	0.40 ± 0.10	1.70 ± 0.10	NR	NR	28.20 ± 15.40	Argentine Sea$^{(2)}$
Arctocephalus australis		[8]	[8]			[8]	
Steller's sea lion	M	<0.10–0.20	NR	NR	NR	24.30–39.10	Hokkaido$^{(3)}$
Eumetopias jubatus		[15]				[15]	(Japan)
Grey seal	B	<0.06	<0.10	<0.60	<0.50	4.70	Cardigan Bay$^{(4)}$
Halichoerus grypus		[1]	[1]	[1]	[1]	[1]	(West Wales)
	M	<0.06	2.50	<0.60	<0.50	43.00	Cardigan Bay$^{(4)}$
		[1]	[1]	[1]	[1]	[1]	(West Wales)
Harbour seal	B	<0.01–0.02	0.9–3.0	<0.50–1.00	NR	3.00–14.00	Dutch Wadden
Phoca vitulina		[3]	[3]	[3]		[3]	Sea (West)$^{(5)}$
	M	NR	NR	1.20 ± 0.30	NR	NR	Britian$^{(6)}$
			[12]				
Ringed seal	M	<0.10–0.40	1.00–1.60	0.20–0.10	NR	14.20–39.50	Greenland$^{(7)}$
Phoca hispida		[29]	[29]	[29]		[29]	(West)
Harp seal	M	0.10	1.80	0.03	NR	NR	Gulf of
Phoca groenlandica		[56]	[50]	[56]			St Lawrence$^{(8)}$
Ribbon seal	M	<0.10–0.30	NR	NR	NR	NR	Okhotsk Sea$^{(9)}$
Phoca fasciata		[16]					
Weddell seal	M	<0.10–0.30	0.90–1.00	NR	NR	33.70–39.60	Antarctic$^{(10)}$
Leptonychotes weddellii		[2]	[2]			[2]	
Leopard seal	B	0.12	NR	0.34	NR	NR	Australia$^{(11)}$
Hydrurga leptonyx		[1]		[1]			
	B	0.54	2.30	0.51	8.39	2.33	South Africa$^{(12)}$
		[1]	[1]	[1]	[1]	[1]	
	M	NR	NR	0.07	NR	NR	Australia$^{(11)}$
				[1]			
	M	<0.10	0.40–1.20	NR	NR	14.80–49.30	Antarctic$^{(10)}$
		[15]	[15]			[15]	
Elephant seal	M	0.40	NR	7.11	NR	35.60	Antarctic$^{(10)}$
Mirounga leonina		[1]		[1]		[1]	

B, blubber. M, muscle. [], sample size. NR, not recorded.

References: (1) present study; (2) Gerpe *et al.,* (1990); (3) Hamanaka *et al.,* (1982); (4) Morris *et al.,* (1989); (5) Duinker *et al.,* (1979); (6) Roberts *et al.,* (1976); (7) Johansen *et al.,* (1980); (8) Ronald *et al.,* (1984); (9) Hamanaka *et al.,* (1977); (10) Thompson (1990); (11) Kemper *et al.,* (1994); (12) Stewardson (unpubl. data).

In South Africa, DDT was withdrawn from the market as an agriculture remedy in 1976; however, it is still used for malaria control. In March/April 1998, the government announced the phasing out of all stocks. There is no official limit on PCBs in South Africa. It was conceded that international market forces would eventually determine their use and availability. Although it would take a considerable amount of time before restrictions and prohibitions on the production and use of organochlorines will take effect in this region, a significant decline in t-DDT has already been observed in inshore waters, e.g., t-DDT concentrations in the inshore bottlenose dolphin, *Tursiops truncatus,* declined significantly from 1980 to 1987 (de Kock *et al.*, 1994). Recent studies of fish and bivalves in the Durban outfalls region confirm that DDT and PCBs are slowly disappearing (EPC, 1998). Only dieldrin and heptachlor are found with any regularity (EPC, 1998).

CONCLUSION

The interpretation of the significance of observed concentrations of heavy metals and organochlorine compounds in the blubber of the Cape fur seal is difficult because the coverage of samples has been very limited and our understanding of pollutants in pinnipeds is still in its infancy. Information on contaminants in healthy pinnipeds is sparse, therefore, authors frequently compare their results with terrestrial laboratory animals or with those from emaciated (beached) pinnipeds.

Considering that pinnipeds differ anatomically and physiologically from terrestrial mammals, pollutants will not have the same toxicity, thus comparisons between the two groups should be made with caution (Skoch, 1990). Even within

Table 12.4 ***Chlorinated hydrocarbon residue concentrations in the blubber of adult Cape fur seals from Southern Africa, 1974–1995.*** **Concentrations are given as the mean and range in µg/g wet wt.**

Date	No.	PCB	DDE	TDE	DDT	t-DDT	Area
1974–75	9	0.13 ND–1.17	1.25 0.02–7.69	0.09 ND–0.54	0.04 ND–0.28	1.38 –	Namibia(1)
1974–75	8	2.79 0.37–5.88	1.45 0.17–3.52	0.36 ND–1.26	1.21 0.14 –3.39	3.02 –	South Africa(1) (south west coast)
1978–80	4*	1.80 0.39–3.49	9.50 2.23–23.03	ND ND	2.40 0.09–7.90	11.30 –	South Africa(2) (east coast)
1993–95	12	ND	ND	ND	ND	ND	South Africa(3) (east coast)

* males and females greater than 1.3 m in length.
ND, not detected.
tDDT = DDT + DDE + TDE.
References: (1) Henry (unpubl. report); (2) Cockcroft & Ross (1991); (3) Present study.

different groups of marine mammals there are significant differences in the ability to metabolise contaminants (Wells *et al.*, 1997). Interpretation can be further complicated by factors such as the seal's age, sex, reproductive condition, size, health condition, feeding habits and geographic location, all of which may influence the total contaminant burden (Reijnders, 1980; Eisler, 1981; Storr-Hansen *et al.*, 1995; Wells *et al.*, 1997).

Information derived from emaciated pinnipeds may also be misleading because metals tend to leach from decomposing tissue of stranded animals (Skoch, 1990), and, if there is a decline in body condition prior to stranding, absolute concentrations of chlorobiphenyl congeners may increase, while some metabolisable chlorobiphenyls may decrease (Boon *et al.*, 1994). Furthermore, comparisons with other data-sets may be erroneous due to methodological differences.

With these limitations in mind, we conclude that the levels of toxic contaminants in the blubber of seals from the Eastern Cape coast of South Africa were generally low compared with those reported from species in other geographic locations, with the exception of Cu and Ni. There is no evidence that the elevated levels of Cu and Ni reported in this study would pose a serious threat to the health of individual animals; however, high concentrations of these metals may be sufficient to result in some additional stress to animals when they mobilise their lipid reserves during illness or starvation. Nickel and Cd concentrations appeared to increase with age; however, small sample size prevented statistical analysis.

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CHAPTER 13

Endoparasites of the Cape fur seal *Arctocephalus pusillus pusillus* from the Eastern Cape coast of South Africa

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ABSTRACT

A total of 53 Cape fur seals, *Arctocephalus pusillus pusillus*, collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34˚ 03'S, 23˚ 24'E) and East London (33˚ 03'S, 27˚ 54'E) from 1992 to 1995, was examined for blubber and stomach parasites. Forty three of these seals (81%) harboured stomach parasites, and 13 (25%) harboured blubber parasites. Nine parasite taxa were identified. Helminth species included adult cestodes *Diphyllobothrium* sp., larval cestodes, *Hepatoxylon trichiuri* and *Phyllobothrium delphini*; nematodes, *Anisakis physeteris*, *Anisakis simplex*, *Contracaecum ogmorhini*, *Contracaecum* sp. and *Hysterothylacium* sp. and an acanthocephalan, *Corynosoma* sp. Three of these taxa, *Hepatoxylon trichiuri, Anisakis physeteris*, and *Hysterothylacium* sp., were accidental parasites. Scanning electron microscope examination confirmed the identity of *Contracaecum ogmorhini* and suggests that earlier studies may have incorrectly identified this nematode as *Contracaecum osculatum*. The prevalence and diversity of endoparasitism was higher in older seals. Intensity of infection was generally higher in stranded animals than in healthy animals incidentally captured in trawl nets. The endoparasites found in the present study did not appear to contribute to the mortality of Cape fur seals, at least in the population from which the examined specimens were taken. Although the anisakine nematodes, *Contracaecum* sp. and *Anisakis* sp., are potentially pathogenic, severe pathological changes were limited to small gastric lesions in the stomachs of three individuals.

INTRODUCTION

Ecologists have recently acknowledged the importance of parasites in the dynamics of populations (McCallum & Dobson, 1995). Some pinniped parasites, particularly certain Nematoda, may act as significant pathogens and cause mortality, or render their host more susceptible to other infectious diseases and environmental stresses (Siniff, 1981; Bray, 1986). For example, unusually high burdens of lungworm, *Filaroides decorus,* are responsible for considerable mortality among young Californian sea lions, *Zalophus californianus* (Sweeney & Gilmartin, 1974; Geraci & St. Aubin, 1986). Hookworms, *Uncinaria lucasi*, can cause haemorrhagic enteritis and anaemia, and have been recorded as a major cause of death in northern fur seal pups, *Callorhinus ursinus* (Olsen, 1958; Geraci & St. Aubin, 1986). Anisakine nematodes, *Contracaecum* sp. and *Anisakis* sp., are frequently associated with gross lesions in the gastrointestinal tract and are assumed to be important in the mortality of the northern fur seal (Keyes, 1965) and the Hawaiian monk seal, *Monachus schauinsladi* (Whittow *et al*., 1979). A high degree of pathogenicity of the anisakine nematode, *Pseudo-terranova decipiens*, has been demonstrated experimentally in captive harbour seals, *Phoca vitulina* (McClelland, 1976, 1980*a*). Although the deleterious effects of some pinniped parasites are known, the information is fragmentary (Geraci & St. Aubin, 1986). Because of difficulties involved in conducting longitudinal studies on wild pinniped populations, most parasitic studies have been based on chance findings rather than systematic survey work. Animals may return to sea for considerable periods; weak seals may leave the herd and become more vulnerable to predation; strandings often occur in remote places and fresh carcasses are soon scavenged.

The Cape fur seal, *Arctocephalus pusillus pusillus,* is the only indigenous breeding pinniped in southern Africa. It breeds at 25 colonies from Black Rocks (lat. 33° 50'S, long. 26° 15'E) on the south-east coast of South Africa, to Cape Cross (lat. 21° 46'S, long. 13° 57'E), Namibia. Current population size is estimated to be 1.5 to 2 million (Butterworth & Wickens, 1990). On the south-east coast, where two breeding colonies occur (Seal Island, Mossel Bay; Black Rocks, Algoa Bay), population levels are declining (SFRI, unpubl. data; Stewardson, unpubl. data), underlying the immediate need to document the biology of these top predators and evaluate potential threats.

The Cape fur seal is host to a wide variety of endoparasites: the cestodes *Diphyllobothrium atlanticum, Phyllobothrium delphini*, *Anophryocephalus anophrys*, and *Taenia solium*; the nematodes, *Contracaecum* spp. (*ogmorhini* and/or *osculatum*), *Anisakis simplex;* two acanthocephalans, *Corynosoma villosum* and *C. australe* (Rand, 1956, 1959; King, 1964, 1983; Delyamure & Parukhin, 1968; Dailey & Brownell, 1972; Dailey, 1975; Testa & Dailey, 1977; Arundel, 1978; De Graaf *et al.*, 1980; Medonca, 1984; Warneke & Shaughnessy, 1985; Pansegrouw, 1990). However, there are few published records of parasite burdens or pathogenicity in this species. Records are largely incomplete, with dispersing juvenile casualties being reported most frequently in the literature.

The present paper documents endoparasites recovered from the blubber and stomach of Eastern Cape fur seals. Parasite taxa are separated into obligate and accidental (aberrant) parasites. The relationship between prevalence of infection and host age is examined; differences between the intensity of infection in animals stranded or caught incidentally as by-catch are investigated; potential transmission pathways of larvae are reviewed, and evidence of pathological manifestations assessed.

MATERIALS AND METHODS

Four females and 49 male Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34˚ 03'S, 23˚ 24'E) and East London (33˚ 03'S, 27˚ 54'E), from July 1992 to August 1995 (Fig. 13.1). Fresh carcasses of animals drowned in nets were removed from commercial trawl vessels, and 20 stranded animals were collected from local beaches. Routine necropsies were performed and biological parameters recorded based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). Each seal was incised ventrally, from the throat to the anus. The subcutaneous blubber layer was systematically dissected. Parallel incisions were made over the entire adipose layer, exposing the underlying muscle. Adipose tissue was manipulated to expose nodules containing encysted cestodes. The seals were dissected further and the stomach opened. Parasites were removed from partially digested food items and from the gastric mucosa. Unattached specimens were collected in a 500 µm mesh sieve. Blubber and stomach parasites were stored in 70% alcohol for subsequent identification.

Cestodes were stained in Mayer's paracarmine, dehydrated in alcohol and mounted in Canada balsam. Acanthocephalans and nematodes were examined as temporary mounts in Beechwood creosote and lactophenol, respectively. Additional specimens of *Contracaecum* preserved in 4% phosphate buffered formalin solution were rinsed in distilled water and then transferred to 70% alcohol for approximately 5 days. Samples were hydrated in an alcohol series and placed in distilled water where they were cleaned with a fine brush and sonicated. The specimens were then dehydrated in an ethanol series and subject to critical point drying. Anterior and posterior ends of individual nematodes were mounted on stubs with silver dag, sputter-coated with approximately 40 *nm* of gold and viewed using a Hitachi, S-2500 scanning electron microscope.

Endoparasites were identified at the Parasitic Worms Division, The Natural History Museum, London, and the Division of Helminthology, Onderstepoort Veterinary Institute, Pretoria. Nematodes

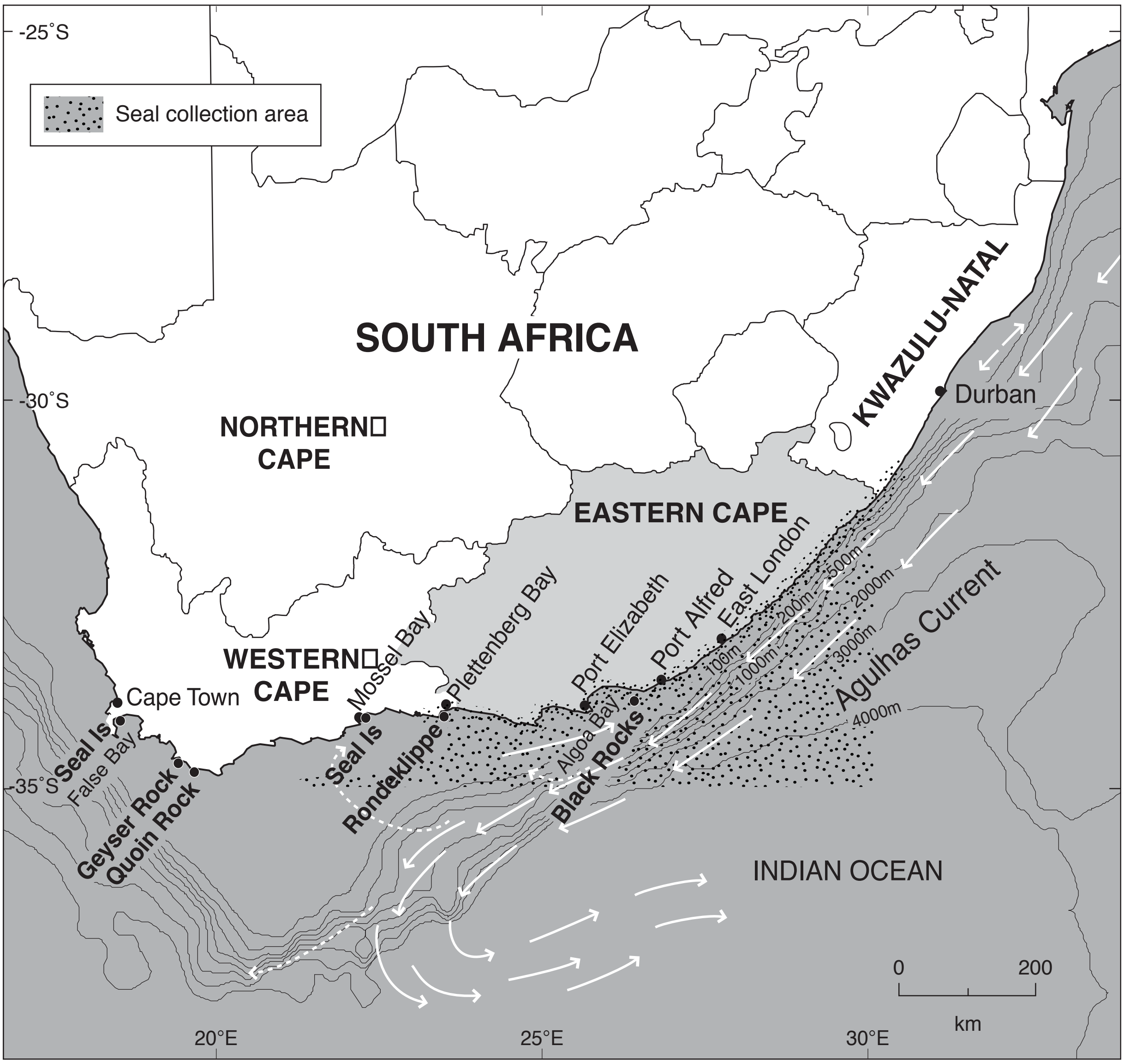

Fig. 13.1 The breeding range of Cape fur seals, *Arctocephalus pusillus pusillus*, along the south coast of southern Africa. Seals (n = 53) were collected from the Eastern Cape coast.

were classified as third- or fourth-stage larvae (L_3 or L_4), adult male or adult female. Total counts (n = 29 seals) were compiled for *Anisakis simplex, Contracaecum ogmorhini,* and *Phyllobothrium delphini*. Specimens were deposited in the Port Elizabeth Museum (PEM), and the Division of Helminthology, Onderstepoort Veterinary Institute, South Africa. Voucher specimens are listed in Appendix 13.1.

Seals were aged from counts of incremental lines observed in the dentine of tooth sections. Upper canines were sectioned longitudinally using a circular diamond saw. Sections were ground down to 280–320 µm, dehydrated, embedded in resin and viewed under a stereomicroscope in polarised light. Interpretation of incremental lines followed Oosthuizen (1997), assuming a birth date of 1 December (Shaughnessy & Best, unpubl. report).

For parasite ecological terminology, the recommendations of Margolis *et al.*, (1982) were used.

RESULTS

Of the 53 Cape fur seals examined, 43 (81%) harboured stomach parasites and 13 (25%) harboured blubber parasites (Table 13.1). Although identification could not always be made to species level, a total of nine taxa was identified. Helminth species included the cestodes *Diphyllobothrium* sp., *Hepatoxylon trichiuri* and *Phyllobothrium delphini*; the nematodes *Anisakis physeteris*, *Anisakis simplex*, *Contracaecum ogmorhini*, *Contracaecum* sp. and *Hysterothylacium* sp.; and an acanthocephalan, *Corynosoma* sp. The most prevalent species recovered from Cape fur seals were the nematodes, *Contracaecum ogmorhini* (58%) and *Anisakis simplex* (51%), and the larval cestode *Phyllobothrium delphini* (25%) (Table 13. 1).

Table 13.1 ***Endoparasites recovered from the blubber and stomach of Cape fur seals, Arctocephalus pusillus pusillus - prevalence and diversity of infection***

Parasite species	**Locality in host**	**Prevalence**[a]	**Intensity**[b] $\overline{X}$ **(range)**
Platyhelminthes: Cestoda			
Adult *Diphyllobothrium* sp.	Stomach	1 (2%)	–
Larval *Hepatoxylon trichiuri*	Stomach	4 (8%)	–
Larval *Phyllobothrium delphini*	Blubber	13 (25%)	26 (2–211; *n* = 12)
Aschelminthes: Nematoda			
Anisakis simplex	Stomach	27 (51%)	71 (1–271; *n* = 12)
Anisakis physeteris	Stomach	10 (19%)	–
Contracaecum ogmorhini	Stomach	31 (58%)	17 (2–95; *n* = 20)
Contracaecum sp.	Stomach	1 (2%)	–
Hysterothylacium sp.	Stomach	1 (2%)	–
Acanthocephala:			
Corynosoma sp.	Stomach	1 (2%)	–

Total no. of seals examined: 53[c]
No. with worms in blubber 13 (25%)
No. with worms in stomach 43 (81%)

[a] Prevalence of infection: the percentage of individual seals infected with a particular parasite species divided by the number of seals examined.
[b] Intensity of infection: the number of individuals of a particular parasite species found in each infected seal. Mean values, range and the number of seals on which total worm counts were conducted.
[c] Seal (PEM2379) was not examined for blubber parasites, i.e., 52 examined for blubber parasites.

Cestoda

Three adult worms, *Diphyllobothrium* sp., were recovered from the stomach of a healthy eight-year-old bull. Worms had presumably migrated from the small intestine postmortem (R. Bray, pers. comm.). These specimens are thought to be *D. atlanticum* (see Schmidt, 1986), a species recovered from *A. p. pusillus* previously (Delyamure & Parukhin, 1968; Warneke & Shaughnessy, 1985; Pansegrouw, 1990). Worms were free in the lumen of the stomach.

Plerocercoids of the trypanorhynchan cestode, *Hepatoxylon trichiuri,* were recovered from the stomachs of four adult bulls. The plerocercoids were free in the lumen of the stomach.

The larval tetraphyllideans, *Phyllobothrium delphini,* were found in 13 (25%) of the seals examined. Intensity of infection ranged from two to 211. Plerocercoids were embedded in the subcutaneous blubber (Fig. 13.2), in the caudal ventral abdomen of the host, predominantly around the genitalia.

Nematoda

Anisakis simplex was found in the stomachs of 27 (51%) Cape fur seals. Intensity of infection ranged from one to 271. With the exception of 17 adult worms recovered from a very thin stranded two-year-old cow, and a single specimen from a stranded three-year-old male, all specimens were third- and fourth-stage larvae. Adult worms were predominantly females. Worms were either attached to the stomach mucosa or free in the lumen of the stomach.

Third stage larvae, morphologically similar to *Anisakis physeteris,* were recovered from the stomachs of 10 seals. Larvae were free in the lumen of the stomach.

Contracaecum ogmorhini (Fig. 13.3) was recovered from the stomachs of 31 (58%) Cape fur seals. Intensity of infection ranged from two to 95. Both adults and fourth-stage larvae were found. Adult worms were predominantly females. Unidentified third-stage larvae (*Contracaecum* sp.) were recovered from the stomach of

Table 13. 2 *Endoparasites recovered from the Cape fur seal, Arctocephalus pusillus pusillus - prevalence of infection and host age*

Age group (years)	No. of seals examined	Total prevalence[a]	No. of parasite taxa $\bar{X}$ (range)
1–2	6	2 (33%)	range 0–1
3–4	6	4 (67%)	1 (0–2)
5–6	7	7 (100%)	3 (2–4)
7–8	24	24 (100%)	2 (1–5)
9–10	6[b]	6 (100%)	2 (1–3)
≥ 11	3	3 (100%)	2 (1–2)
Total	**52**		**9**

[a] Total prevalence of infection: the percentage of individual seals infected with parasites divided by the number of seals examined.

[b] Seal (PEM2379) aged 10 years was excluded from analysis, i.e., blubber parasites not examined.

a seven-year-old cow. Worms were either attached to the stomach mucosa or free in the lumen of the stomach.

Hysterothylacium sp. (one adult female worm) was recovered from the lumen of the stomach of a six-year-old cow.

Acanthocephala

One cystacanth of *Corynosoma* sp. in poor condition, was recovered from the lumen of the stomach of an old bull. Acanthocephalans are generally found in the stomach or small intestine of otariids (Smales, 1986), and also in piscivorous birds. Accidental ingestion seems unlikely (D. Gibson, pers. comm.).

Fig. 13.2 Larval tetraphyllideans, *Phyllobothrium delphini*, embedded in the subcutaneous blubber of a Cape fur seal, *Arctocephalus pusillus pusillus*.

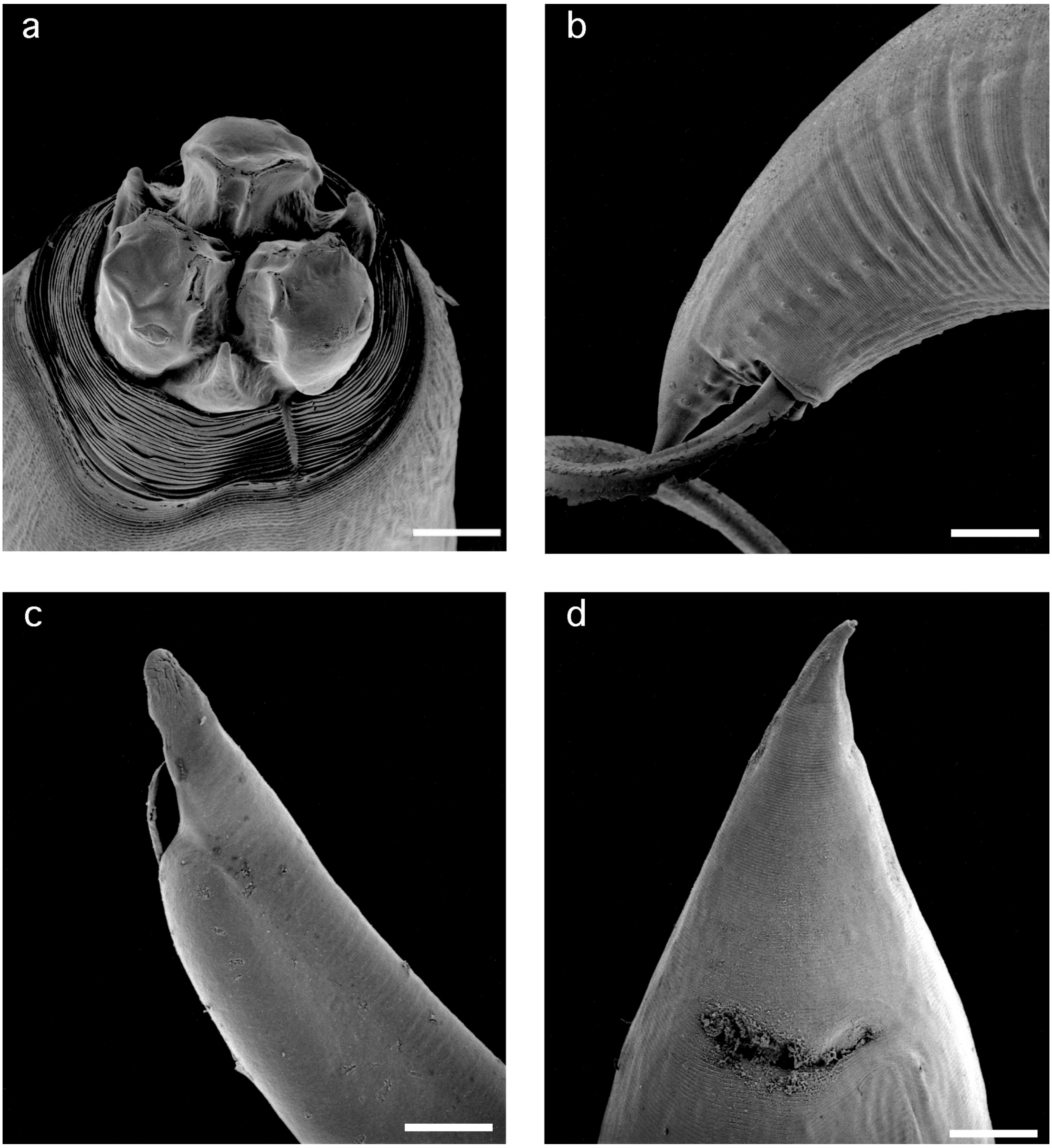

Fig. 13.3 SEM micrographs of *Contracaecum ogmorhini* from the stomach of a Cape fur seal, *Arctocephalus pusillus pusillus*.
(a) Anteroventral view of the head of a male worm. Scale bar: 100µm.
(b) Posterior portion of male worm showing conical tail with protruding spicules. Scale bar: 120µm.
(c) Distal end of spicule. Scale bar: 30µm.
(d) Ventral view of female tail. Scale bar: 150µm.

Prevalence of infection and host age

The total prevalence of infection increased with increasing age of the seals (Table 13.2). Parasites were recovered from 33% of seals in the 1–2 year old age group and 67% in the 3–4 year old age group. All seals ≥ five years of age harboured endoparasites. Younger seals harboured fewer species of parasites (0–1), whereas older seals (≥ five years of age) harboured up to five parasite species (Table 13.2).

Intensity of infection and host age

The relationship between host age and intensity of infection for *Phyllobothrium delphini* and *Anisakis simplex* could not be established as sample size per age group was too small. However, preliminary worm counts suggested that the degree of infection of *Contracaecum ogmorhini* was slightly higher in older animals. Up to 95 nematodes (*Contracaecum ogmorhini)* were found in the stomachs of older seals (mean 12; range 0–95), whereas seals ≤ four years carried less than 30 nematodes (mean eight; range 0–29).

Table 13.3 ***Endoparasites recovered from the Cape fur seal, Arctocephalus pusillus pusillus - comparison between fishery by-catch and stranded seals.*** **All seals are > 5 years of age**

Parasite species	**Stranded sub sample Intensity**[a] **$\bar{X}$ (range)**	**By-catch sub sample Intensity**[a] **$\bar{X}$ (range)**
Phyllobothrium delphini	42 (0–211, *n* = 12)	8 (0–27, *n* = 18)
Anisakis simplex	271[b]	53 (0–235, *n* = 18)
Contracaecum ogmorhini	19 (0–95, *n* = 12)	15 (0–34, *n* = 18)

[a] Intensity of infection: the number of individuals of a particular parasite species found in each infected seal. Mean values, range and the number of seals on which total worm counts were conducted.

[b] Although *A. simplex* was recovered from two stranded seals (Appendix 13.1), one animal was less than five years of age.

Stranded and fishery by-catch sub samples

Parasite counts were conducted on 18 seals recovered from commercial trawl nets, and 12 seals collected from local beaches. Seals less than five years of age were excluded from analysis. All trawled specimens were in good body condition, i.e., healthy animals netted on feeding grounds. Stranded specimens were generally in poor body condition and/or injured, i.e., fresh carcasses collected from local beaches (Appendix 13.1). Results are presented in Table 13.3. Although some healthy seals carried high numbers of parasites (e.g., 235 *Anisakis simplex* in an eight-year-old male), intensity of infection was generally lower than in stranded animals.

DISCUSSION

Accidental parasites

Nine parasite taxa were recovered from the Cape fur seals, of which *Hepatoxylon trichiuri, Anisakis physeteris* and *Hysterothylacium* sp. were accidental parasites.

Hepatoxylon trichiuri

Plerocercoids of *Hepatoxylon trichiuri* were recovered from the stomachs of four adult bulls. The bulls had been feeding on *Trachurus trachurus*, *Lepidopus caudatus* and *Merluccius* sp. In southern African waters, *H. trichiuri* has been recorded in Cape hakes, *Merluccius capensis* and *M. paradoxus* (Botha, 1986), and kingklip, *Genypterus capensis* (Payne, 1986). Although the entire life history of this cestode has yet to be elucidated, *H. trichiuri* is presumably transferred up the food chain through copepod crustaceans to teleosts (intermediate hosts) (Botha, 1986). Adult worms have been found in *Lamna nasus* (Dollfus, 1942), *Isurus oxyrinchus* (Dollfus, 1942; Beveridge & Campbell, 1996) and *Carcharodon carcharias* (Beveridge & Campbell, 1996).

Anisakis physeteris

Third stage larvae, morphologically similar to *Anisakis physeteris,* were recovered from the stomachs of 10 seals. *Anisakis physeteris,* a cetacean parasite (Davey, 1971), has not been recorded in *Arctocephalus* previously. This suggests that Cape fur seals often ingest infected fish and/or squid species also eaten by east coast cetaceans, e.g., *Kogia breviceps* and *K. simus* (Ross, 1984).

Hysterothylacium sp.

One adult female worm, *Hysterothylacium* sp.*,* was recovered from the stomach of a six-year-old cow. In the adult stages, *Hysterothylacium* is normally found in the gut of marine fish (Anderson, 1992); therefore, infection was accidental. Although the undigested remains of *Merluccius* spp. were found in the stomach of the seal, according to Botha (1986), *Hysterothylacium* is not a known parasite of Cape hakes. No other dietary remains were found.

Life cycles and pathogenicity of obligate endoparasites

Diphyllobothrium spp.

Adult *Diphyllobothrium* spp. are found in fish-eating birds and mammals (Bray *et al.*, 1994). *Diphyll-obothrium atlanticum* is the only valid record of a pseudophyllidean cestode for *A. p. pusillus,* and is usually found in the posterior 50 cm of the small intestine, and the entire length of the large intestine; the primary site of infection appears to be the middle and anterior third of the large intestine (Pansegrouw, 1990). In Cape fur seals from Namibia, the prevalence of *D. atlanticum* is 65% (84 seals examined), with no significant differences in the prevalence between male and female hosts (Pansegrouw, 1990).

In marine mammals, infection presumably occurs through the ingestion of the secondary intermediate host, an infested teleost. However, the only known life cycles are those of *Diphyllobothrium latum, D. dendriticum and D. sebago* (e.g., Vik, 1964; Weber, 1991).

Diphyllobothrium species have been implicated in human infection in countries where fish is consumed raw, slightly cooked or salted; when ingested by humans, larvae may invade the gastrointestinal tract and cause disease (Geraci & St. Aubin, 1986; Oshima & Kliks, 1986). Although the pathological significance of *Diphyllobothrium* infections in pinnipeds has not been established clearly, infection with mature worms is usually innocuous (e.g., Rees, 1967; Arundel, 1978). In severe cases, parasites can encyst in the colonic wall, obstruct the lumen of the gut and/or may prevent weight gain (Sweeney, 1973; Clausen, 1978; Arundel, 1978; Cordes & O'Hara, 1979; Geraci & St Aubin, 1986).

Phyllobothrium delphini

Larval *Phyllobothrium delphini* has been recorded from a range of cetacean and pinniped hosts (Testa & Dailey, 1977; Schmidt, 1986), including *Arctocephalus pusillus doriferus* (see Arundel, 1978; Warneke & Shaughnessy, 1985), *Arctocephalus tropicalis* (see King, 1964; Bester, 1989; Stewardson, unpubl. data) and *A. p. pusillus* (Pansegrouw, 1990; present study). The plerocercoids observed in the present study were concentrated in the abdominal blubber. The same pattern of distribution was observed in Cape fur seals from Namibia (Pansegrouw, 1990). In Namibia, the prevalence of pleroceroids in Cape fur seals is 75% (90 seals examined) with no significant differences in the prevalence between male and female hosts (Pansegrouw, 1990). This is much higher than the overall prevalence for Eastern Cape seals (25%), possibly reflecting differences in the age and/or diet of individual hosts.

How marine mammals become infected with *Phyllobothrium delphini* is still a matter of conjecture; however infection may occur through the procercoid taken with a teleost or squid that had recently fed on an infected crustacean (Testa & Dailey, 1977). *Phyllobothrium delphini* presumably complete their life cycle in white sharks *Carcharodon carcharias*, and mackerel sharks *Isurus oxyrhynchus* (Arundel, 1978). Along the south-east coast of southern Africa, white sharks frequently prey on Cape fur seals; attacks are usually from behind, thus the seal is initially bitten on the lower body (Stewardson, unpubl. data). Concentration of larvae within the vulnerable abdominal tissues may reflect migration from the gut and provide some advantages in transmission to sharks (Geraci & St. Aubin, 1986).

Infection is a focal chronic inflammation with an acute suppurative component surrounding encysted larvae (R. Norman, pers. comm.), which may have some metabolic cost to the animal, e.g., in females, heavy infection of the abdominal blubber, near the mammary glands, may possibly retard lactation and affect pup growth (Pansegrouw, 1990). Although some seals carried large numbers of larvae, animals were generally in good body condition and did not appear to be adversely affected by the infection.

Anisakis simplex

Anisakis simplex is a cosmopolitan species found in all sub-families of pinnipeds (Arundel, 1978); it is a known parasite of *Arctocephalus pusillus doriferus* (see Arundel, 1978; Warneke & Shaughnessy, 1985), *A. tropicalis* (see Shaughnessy & Ross, 1980; Bester, 1989; Stewardson, unpubl. data), *A. australis* (see Davey, 1971) and *A. p. pusillus* (Pansegrouw, 1990; present study). In Namibia, the prevalence of *Anisakis simplex* in Cape fur seals was 91% (11 seals examined), with a higher prevalence of nematode infection in males than in females (Pansegrouw, 1990). This is much higher than the overall prevalence for Eastern Cape seals (51%).

The role of pinnipeds in transmitting *Anisakis simplex* to commercially valuable fish in Europe and Japan, is of considerable economic and medical importance (Smith & Wootten, 1978; Desowitz, 1986; Geraci & St. Aubin, 1986; Malouf, 1986; Oshima & Kliks, 1986; Huang & Bussieras, 1988). Infected commercial fish and squid may cause anisakiasi in humans if eaten raw, slightly cooked or salted. Unlike *Diphyllobothrium* sp*.,* the larval form can persist temporarily in the human gastrointestinal tract (Oshima & Kliks, 1986).

In marine mammals, anisakids may cause inflammation and/or ulceration of the stomach, gastritis, enteritis, diarrhoea, dehydration and anaemia (Wallach, 1972; Cattan *et al*., 1976; Stroud & Roffe, 1979; McClelland, 1980*a*; Geraci & St. Aubin, 1986; Bester, 1989; Smith, 1989; Pansegrouw, 1990; Brattey & Ni, 1992). Chronic infection may lead to perforation of the alimentary tract, peritonitis and death (Young & Lowe, 1969; Geraci & St. Aubin, 1986). In the present study, small gastric lesions, associated with larval *A. simplex* and *Contracaecum ogmorhini*, were observed in three adult animals. These animals were otherwise in good condition (incidental by catch). Nodules resembling small ulcers associated with *Contracaecum* sp. have been reported in Cape fur seals from Sinclair Island, and appear to be common in older males (Rand, 1959).

Eggs of *Anisakis simplex*, passed in the faeces of marine mammals, develop into free-swimming sheathed second-stage larvae (Smith & Wootten, 1978). Larvae are ingested by the first intermediate host (copepods, euphausiids and decapods) and develop into third-stage larvae (Polyanskii, 1961; Van Thiel, 1966; Smith, 1971; Beverley-Burton & Pippy, 1978) which are eaten by the second intermediate host (teleost fish or squid) (Clarke, 1966; Anderson, 1992). Transmission of infective larvae to pinnipeds and cetacea (definitive hosts) occurs through the consumption of infected fish, crustaceans or squid (Anderson, 1992). In marine mammals, infective larvae and adult worms are normally found free in the stomach or attached to the gastric mucosa (Geraci & St. Aubin, 1986).

Dominant prey species of the Cape fur seal (David, 1987; Stewardson, unpubl. data), Cape hake and anchovy (*Engraulis capensis*), are known to carry *Anisakis* larvae (Hennig, 1974; Botha, 1986). Cape hake feed extensively on euphausiids when young and have a piscivorous and cannibalistic diet as adults (Botha, 1980). As the prevalence of larval infection in Cape hakes is high, we suggest that this teleost is a likely source of infection in the seals examined. Cape fur seals do not appear to contribute significantly in the transmission of *A. simplex* to commercially valuable fish off the Eastern Cape coast (e.g., only two debilitated seals harboured adult worms). Cetacea are presumably the most common host to species of *Anisakis* (Young, 1972; Smith & Wootten, 1978).

Contracaecum ogmorhini

Contracaecum 'osculatum' has been reported in *Arctocephalus p. pusillus* (Rand, 1956, 1959; Dailey & Brownell, 1972; Warneke & Shaughnessy, 1985), *A. p. doriferus* (Delyamure, 1968; Dailey & Brownell, 1972; Arundel, 1978; Warneke & Shaughnessy, 1985), *A. tropicalis* (Dailey & Brownell, 1972; Shaughnessy & Ross, 1980; Bester, 1989), *A. forsteri* (Arundel, 1978) and *A. australis* (Delyamure, 1968; Dailey & Brownell, 1972). In Namibia, the prevalence of *Contracaecum* spp. in Cape fur seals is 100% (11 seals examined), with a higher prevalence of nematode infection in males than in females (Pansegrouw, 1990). This is much higher than the overall prevalence for Eastern Cape seals (58%).

Until recently, *Contracaecum osculatum* was thought to have a worldwide distribution. However, studies by Fagerholm & Gibson (1987) found that *C. osculatum* is essentially a parasite of phocids, and *C. ogmorhini* is essentially a parasite of otariids, specifically *Zalophus californianus, Eumetopias jubatus* and *A. tropicalis.* Therefore, there is considerable doubt associated with the above records (Fagerholm & Gibson, 1987). In the present study, it was possible to distinguish *C. ogmorhini* by examining the distribution of pre- and post-cloacal papillae in the male using SEM, according to Fagerholm & Gibson's criteria (1987). Unlike *C. osculatum,* male *C. ogmorhini* have two rows of 23–49 subventral precloacal papillae and seven postcloacal pairs of papillae (Fagerholm & Gibson, 1987). The postcloacal pairs are arranged as follows: two large subventral pairs close to the cloaca, side by side; two subventral pairs and two sublateral pairs in the posterior half of the tail, and a single sublateral pair (Fagerholm & Gibson, 1987). SEM micrographs of *C. ogmorhini* are presented in Fig. 13.3 *Contracaecum* sp. recovered from *Arctocephalus tropicalis* stranded along the south-east coast of South Africa (1992–1994), were also identified as *C. ogmorhini* (i.e., 14 seals collected by Stewardson; parasites identified by Fourie). We therefore suggest that the above records (Rand, 1956, 1959; Delyamure, 1968; Dailey & Brownell, 1972; Arundel, 1978; Warneke & Shaughnessy, 1985; Bester, 1989) are probably *C. ogmorhini* and not *C. 'osculatum'* (but see Pansegrouw, 1990).

The life cycle of *Contracaecum ogmorhini* is not known, but is presumably similar to *C. osculatum baicalensis* (see Mozgovi & Ryzhikov, 1950) in which larvae are transferred through the sand hopper *Macrohectopus branickii* (intermediate host) and the yellow goby *Cottomephorus grewingki* (paratenic host), to the Baikal seal *Phoca sibirica* (definitive host) (Delyamure, 1968). The cycle may be completed with an optional invertebrate paratenic host and a single fish intermediate host (Anderson, 1992; Køie & Fagerholm, 1995).

Small gastric lesions, associated with *C. ogmorhini* (adults), were observed in three animals; however, gross pathological changes were minimal. *Contracaecum ogmorhini* may be responsible for abnormal tissue migration such as brain infestation in the Californian sea lion (Flores-Barroeta *et al.*, 1961) and, in extreme cases, may cause severe ulceration and death (Geraci & St. Aubin, 1986).

Corynosoma sp.

One acanthocephalan cystacanth in poor condition, *Corynosoma* sp., was recovered from the stomach of an old bull. *Corynosoma* sp. (e.g., *C. australe*, *C. villosum* and *C. strumosum*) have been previously recorded in the small intestine of *Arctocephalus* sp. (King, 1964; Delyamure & Parukhin, 1968; Arundel, 1978; Shaughnessy & Ross, 1980; Smales, 1986; Pansegrouw, 1990). This species is most likely to be *C. australe* (see Pansegrouw, 1990). In Cape fur seals from Namibia, the prevalence of *C. australe* is 93% (88 seals examined), with no significant differences in the prevalence between male and female hosts (Pansegrouw, 1990).

The development and life cycles of *Corynosoma* have been reviewed by Schmidt (1985). Fusiform eggs, passed through faeces, are ingested by crustaceans (first intermediate host), during which time the acanthella develops and transforms into a cystacanth capable of infecting the definitive host. A paratenic host (i.e., fish) is required for transmission to the definitive host. When the fish is ingested by a seal (definitive host), the cystacanth develops into the adult worm which attaches itself to the wall of the small intestine (Arundel, 1978). The semi-digested remains of *Trachurus trachurus capensis*, *Merluccius* spp., *Scomber japonicus* and *Zenopsis* sp. were recovered from the stomachs of the seals; however, the likely paratenic host could not be established.

Although acanthocephalans may cause lesions that enable other pathogens to become established (Pansegrouw, 1990), the report by Arundel (1978) of an absence of gross lesions in the intestine of *Arctocephalus p. doriferus,* infected with large numbers of *Corynosoma australe,* suggests that infection is not generally detrimental to the host.

Prevalence of infection and host age

The total prevalence of endoparasitism in Cape fur seals increased with host age, from 33% in animals one to two-years of age, up to 100% in animals ≥ five years of age. Similar findings were reported by Lick (1989) who examined the stomachs of 274 harbour seals from the German and Danish Wadden Sea; in these seals, the total prevalence of stomach nematodes increased from 28% in animals less than one-year of age, to 80% in 1–2 years olds, and to 95% in animals more than two-years old. Stomach nematodes infect young harbour seals soon after weaning (4–6 weeks of age). Older seals target highly infected fish species such as *Osmerus eperlanus*, resulting in a high infection rate. However, the rate of infection in 1–2 year-olds is lower than expected and may be attributed to different feeding behaviours (consuming non-infected versus infected fish) or the development of partial resistance (Lick, 1989).

Cape fur seal pups are weaned at 8–12 months and are unlikely to ingest infected fish/cephalopods until they are at least four months of age, when they supplement their milk diet with solids. As the young seals mature, their dietary preferences expand according to experience and opportunities offered (Rand, 1959). Older seals presumably have a greater chance of ingesting infective larvae because of age-related changes in the size or quantity of prey items consumed (Brattey & Ni, 1992). Increased capacity of the stomach among larger seals may enable several species of parasites to occupy the same habitat (Crompton & Joyner, 1980; Brattey & Ni, 1992).

Intensity of infection and host age

Up to 95 nematodes (*Contracaecum ogmorhini)* were found in the stomachs of older seals, whereas seals ≤ four years carried less than 30 nematodes. Similar findings were reported by Rand (1959) who found that adult Cape fur seals harboured as many as 100 nematodes (*Contracaecum* sp.) and yearlings usually carried between 5–10. In harbour seals from the German and Danish Wadden Sea, the intensity of stomach nematodes (*Anisakis simplex; Contracaecum* sp*; Porrocaecum decipiens*) also increased with increasing age of seals (Lick, 1989). Harbour seals less than one year of age usually carried 1–10 nematodes, whereas seals older than two years of age carried as many as 159 nematodes (Lick, 1989).

The intensity of stomach nematodes in older Cape fur seals (*Anisakis simplex* up to 271, and *Contracaecum ogmorhini* up to 95) was not unusually high compared with seals from other regions. For example, high numbers of *Contracaecum* sp. have been reported in Grey seals, *Halichoerus grypus*, from Nova Scotia (*c*. 17 000 nematodes; McClelland, 1980*a*), and in Weddell seals, *Leptonychotes weddellii,* from Antarctica (*c*. 122 000 nematodes; Klöser *et al*., 1992). In subantarctic fur seals from Gough Island, stomach nematodes, *Anisakis simplex, Contracaecum* sp. *and Phyllobothrium decipiens*, ranged between 1–505 (Bester, 1989). In Cape fur seals from Namibia, the mean number of stomach nematodes, *Anisakis simplex, Contracaecum* sp. was 54, with numbers ranging from 0–1 004 (Pansegrouw, 1990).

Stranded and fishery by-catch sub samples

Preliminary observations indicate that in animals ≥ 5 years of age the intensity of infection was generally lower in healthy seals (by-catch) than in stranded animals. Although no histopathological studies were conducted on the stranded animals, gross observations did not suggest that parasitism was a contributing cause of death. Furthermore, several healthy animals (by-catch) had higher parasite burdens than stranded animals and showed no signs of weight loss or emaciation. It is likely that injuries or illness may have prevented seals from capturing adequate food (i.e., stranded sub samples). As their body conditions deteriorated, individuals would have become more vulnerable to disease, resident parasites and predation. In an environment which places heavy demands on thermoregulation, respiration and mobility, these animals would have soon died (see Geraci & St. Aubin, 1986).

Sixty two per cent of stranded seals had food contents in their stomach; however only 15% had fresh remains (i.e., flesh attached to either cephalopod beaks or skeletal material). Therefore, values reported here must be considered as a minimum parasite burden. Other factors which may have reduced observed parasite burdens in healthy and/or stranded seals include regurgitation of undigested otoliths and cephalopod beaks (Stewardson, pers. obs); vomiting during trawl capture or stranding (Lick, 1989); fasting during the annual moult (McClelland, 1980*b*), and postmortem migration of parasites through the nostrils, mouth or rectum (Myers, 1960).

CONCLUSION

The data presented in this study provides the first published records of *Anisakis simplex* and *Contracaecum ogmorhini* for Cape fur seals, and supplement earlier studies, providing additional records of known obligate parasites, *Diphyllobothrium* sp., *Phyllobothrium delphini, Contracaecum* sp. and *Corynosoma* sp. Accidental parasites, *Hepatoxylon trichiuri*, *Anisakis physeteris* and *Hysterothylacium* sp., have not been recorded previously. Scanning electron microscope studies confirmed the identity of *Contracaecum ogmorhini* and suggested that earlier studies may have incorrectly identified this nematode as *Contracaecum osculatum*. The majority of seals examined had stomach parasites and infection was higher among older animals. We suggest that anisakid infection is transmitted to Cape fur seals largely through Cape hakes. The potential transmission pathway of *Diphyllobothrium* sp. could not be established.

The endoparasites isolated in the present study did not appear to contribute to the mortality of Cape fur seals, at least in the population from which our specimens were taken. Although the anisakid nematodes, *Contracaecum* and *Anisakis*, are potentially pathogenic (Desowitz, 1986), no severe pathological conditions were found, other than small gastric lesions in the stomach of three individuals. It is likely that anisakid nematodes are more harmful to diseased or captive seals under stress (Brattey & Ni, 1992). Intensity of infection was generally higher in stranded seals than in healthy seals, captured in commercial trawl nets. Weak and/or injured seals are presumably more vulnerable to parasitism.

Sex and age bias (i.e., predominance of older males in the sample) prevented detailed analysis of the intensity of infection and host age; therefore, ongoing systematic surveys are required. Histopathological studies (patterns of degenerative, inflammatory, and proliferative changes of infected pinniped tissues) are also needed to link parasitism with morbidity and mortality of individuals and populations.

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Appendix 13.1 ***Endoparasites recovered from the Cape fur seal, Arctocephalus pusillus pusillus***

Accession no.[a]	**Sex**	**Date Collected**	**Species isolated**	**By-catch**	**Stranded**[b]
1999	M	20 July 1992	*Anisakis simplex* (Rudolphi, 1809) *Anisakis physeteris* (Baylis, 1923) *Contracaecum ogmorhini* (Johnston & Mawson, 1941) *Hepatoxylon trichiuri* (Holten, 1802) *Phyllobothrium delphini* (Bosc, 1802)	Bc	
2000	M	21 July 1992	*A. simplex* *A. physeteris* *C. ogmorhini*	Bc	
2001	M	21 July 1992	*C. ogmorhini*	Bc	
2002	M	22 July 1992	*A. simplex* *A. physeteris*	Bc	
2003	M	24 July 1992	*A. simplex* *C. ogmorhini*	Bc	
2004	M	25 July 1992	*A. simplex* *A. physeteris* *C. ogmorhini* *Corynosoma* spp.	Bc	
2005	M	11 August 1992	*A. simplex*	Bc	
2006	M	13 August 1992	*A. physeteris*	Bc	
2007*	M	14 August 1992	*C. ogmorhini* *A. simplex*	Bc	
2008	M	14 August 1992	*A. simplex* *A. physeteris* *C. ogmorhini* *Hysterothylacium* sp.	Bc	
2009	M	22 August 1992	*C. ogmorhini* *H. trichiuri*	Bc	
2010	M	22 August 1992	*A. simplex* *A. physeteris* *C. ogmorhini* *H. trichiuri*	Bc	
2011	M	8 September 1992	*A. simplex* *C. ogmorhini* *H. trichiuri*	Bc	
2012	M	9 September 1992	*A. simplex* *C. ogmorhini* *Contracaecum* sp.	Bc	
2013	M	14 September 1992	*A. simplex* *A. physeteris* *C. ogmorhini*	Bc	
2014	M	25 September 1992	*A. simplex* *A. physeteris*	Bc	
2015	F	3 November 1992	*A. simplex* *A. physeteris*	Bc	

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Accession no.[a]	**Sex**	**Date Collected**	**Species isolated**	**By-catch**	**Stranded**[b]
2035*	M	11 March 1993	*A. simplex*		St (I)
2046*	M	19 May 1993	*C. ogmorhini*	Bc	
2047*	M	20 May 1993	*A. simplex* *C. ogmorhini*	Bc	
2048*	M	20 May 1993	*C. ogmorhini* *A. simplex*	Bc	
2051*	M	28 June 1993	*Diphyllobothrium* sp. *A. simplex*	Bc	
2052*	M	28 June 1993	*A. simplex*	Bc	
2053*	M	28 June 1993	*P. delphini* *A. simplex* *C. ogmorhini*	Bc	
2054*	M	29 June 1993	*A. simplex*	Bc	
2055*	M	29 June 1993	*A. simplex*	Bc	
2082*	M	19 July 1993	*P. delphini* *A. simplex* *C. ogmorhini*	Bc	
2087*	M	17 August 1993	*C. ogmorhini* *P. delphini*		St
2134*	M	28 December 1993	*C. ogmorhini*		St (I)
2137*	M	5 January 1994	*C. ogmorhini* *P. delphini*		St
2143*	M	21 January 1994	*P. delphini* *C. ogmorhini*		St (I)
2186*	M	7 April 1994	*C. ogmorhini*		St (I)
2191*	M	4 May 1994	*C. ogmorhini*		St
2197*	M	12 July 1994	*C. ogmorhini*		St (I)
2203*	M	18 July 1994	*C. ogmorhini* *P. delphini*		St (I)
2204*	F	23 July 1994	*C. ogmorhini*	Bc	
2253*	M	27 August 1994	*P. delphini*	Bc	
2254*	M	27 August 1994	*C. ogmorhini* A. *simplex*	Bc	
2256*	M	17 September 1994	*P. delphini* *C. ogmorhini*	Bc	
2257*	M	7 October 1994	*C. ogmorhini* *A. simplex*	Bc	
2258*	M	8 October 1994	*P. delphini*	Bc	
2348*	M	14 November 1994	*C. ogmorhini*	Bc	
2350*	F	13 December 1994	*A. simplex*		St
2379*	M	12 April 1995	*C. ogmorhini*		St
2400*	M	13 July 1995	*P. delphini* *A. simplex*	Bc	
2406*	M	25 July 1995	*P. delphini*		St (I)
2411*	M	24 August 1995	*P. delphini*		St

[a] Accession no., Port Elizabeth Museum (PEM) specimen accession number.

[b] St, stranded seals; St (I), stranded seals with injury, e.g., gun shot wounds, shark bites etc.

* Specimens deposited with the Division of Helminthology, Onderstepoort Veterinary Institute.

CHAPTER 14(a)

Preliminary investigations of shark predation on Cape fur seals *Arctocephalus pusillus pusillus* from the Eastern Cape coast of South Africa

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ABSTRACT

Shark predation on Cape fur seals, *Arctocephalus pusillus pusillus*, from the Eastern Cape coast of South Africa was investigated. Observations were made on an opportunistic basis over a five year period from 1991 to 1996. Evidence of shark predation was obtained from: (i) incidental observations of shark attacks on live Cape fur seals, and (ii) counts of shark bite wounds on the bodies of live and dead seals. In Eastern Cape waters, potential shark predators include the white, *Carcharodon carcharias*; broadnose sevengill, *Notorynchus cepedianus*; bluntnose sixgill, *Hexanchus griseus*; shortfin mako, *Isurus oxyrinchus*; bull, *Carcharhinus leucas*; tiger, *Galeocerdo cuvier*; and dusky, *Carcharhinus obscurus*. Only the white and broadnose sevengill shark have been observed actively feeding on Cape fur seals. Shark bitten seals (n = 33) were observed throughout the year, with coastal records peaking in the autumn/winter period. Adult animals were observed with shark bite wounds more often than young. Wounds were usually located on the lower body, suggesting that attacks were made from behind. Fresh shark bite wounds were found on a minimum of 3.4% of seals found stranded on local beaches, and 0.3% of seals observed at the Black Rocks colony during the breeding season. Although predatory encounters appear to be common, long term studies are required before we can fully assess the extent of shark predation along the Eastern Cape coast. These records are the only known examples of shark inflicted injuries on southern fur seals *Arctocephalus* spp. south of 10°S.

INTRODUCTION

Shark predation is thought to be a significant cause of natural mortality in some species of seals, including the monk seal, *Monachus schauinslandi* (Wirtz, 1968; Kenyon, 1980, 1981; Alcorn & Kam, 1986), northern elephant seal, *Mirounga angustirostris* (Ainley *et al.*, 1981, 1985; Le Boeuf *et al.*, 1982; Klimley *et al.*, 1992), harbour seal, *Phoca vitulina*, and grey seal, *Halichoerus grypus* (Boulva & McLaren, 1979; Brodie & Beck, 1983). Apart from direct mortality, shark predation may significantly lower the survival rate of individual seals (Wirtz, 1968; Johnson & Johnson, 1981; Gilmartin, 1983; Alcorn, 1984), and reduce reproductive success (Ainley *et al.*, 1981; Le Boeuf *et al.*, 1982). It may also influence the timing of the breeding season (Ainley *et al.*, 1985), and influence the selection of preferred pupping habitats (Westlake & Gilmartin, 1990).

The Cape fur seal, *Arctocephalus pusillus pusillus*, is the only pinniped indigenous to southern Africa. It breeds at 25 colonies from Black Rocks (lat. 33° 50'S, long. 26° 15'E) on the south-east coast of South Africa, to Cape Cross (lat. 21° 46'S, long. 13° 57'E), Namibia. Current population size is estimated to be *c.* 1.5 to 2 million (Butterworth & Wickens, 1990). On the south-east coast, where two breeding colonies occur (Seal Island, Mossel Bay; Black Rocks, Algoa Bay), population levels are declining (SFRI, unpubl. data; Stewardson, unpubl. data), underlying the immediate need to document the biology of these top predators, and evaluate potential threats.

Cape fur seals are often observed with fresh shark bite wounds (pers. obs.), and have been found in the stomachs of white sharks, *Carcharodon carcharias* (Cliff, *et al.*, 1989, 1996), bluntnose sixgill sharks, *Hexanchus griseus*, and broadnose sevengill sharks, *Notorynchus cepedianus* (Ebert, 1991*a*, *b*, 1994; M. Smale, pers. comm.). However, the extent and effect of shark predation on the local seal population is not known.

The present paper examines shark predation on Cape fur seals from the Eastern Cape coast of South Africa. Evidence of shark predation was obtained from: (i) observations of shark attacks on live Cape fur seals, and (ii) counts of shark bite wounds on the bodies of live and dead seals. Attack behaviour was inferred from direct observation (interviews with experienced fishermen) and the position of wounds on prey.

MATERIALS AND METHODS

Study area

Data were collected between Plettenberg Bay (34°03'S, 23°24'E) and East London (32°58'S, 27°58'E), with the addition of a few beached animals collected from KwaZulu-Natal (Fig. 14(a).1). Two seal colonies occur in the study area: Black Rocks (Algoa Bay), a breeding colony with *c.* 700 seals (SFRI unpubl. data), and Rondeklippe (Plettenberg Bay), a small non-breeding colony.

Black Rocks consists of a series of five rocky outcrops surrounded by water *c.* 30 m deep. The largest outcrop, the main breeding rock, is 8 360 m^2 and 6 m above mean sea level.

Rondeklippe consists of a rocky platform, covering *c.* 240 m^2. The highest point is *c.* 2.8 m above mean sea level. Water depth is 3.5 m.

Large predatory sharks found off the Eastern Cape coast

A list of predatory sharks known to inhabit Eastern Cape waters and prey on marine mammals was compiled from the FAO species catalogue, *Sharks of the world* (Compagno, 1984). Seven species of sharks have been implicated as predators of marine mammals: the white (Compagno, 1984; Ross, 1984; Cliff, *et al.*, 1989, 1996); broadnose sevengill (Ebert, 1991*a*, *b*; M. Smale, pers. comm.); bluntnose sixgill (Compagno, 1984; Ebert, 1994; M. Smale. pers. comm.); shortfin mako, *Isurus oxyrinchus* (Compagno, 1984; Long & Jones, 1996); bull, *Carcharhinus leucas* (Compagno, 1984; Cockcroft *et al.*, 1989); tiger, *Galeocerdo cuvier* (Cockcroft *et al.*, 1989; Compagno, 1984); and dusky, *Carcharhinus obscurus* (Cockcroft *et al.*, 1989) sharks.

Shark bitten seals

Between May 1992 and November 1994, six day trips were made to Black Rocks to assess the number of seals with signs of shark inflicted injuries. Counts began at 800 hrs from an inflatable boat, *c.* 10 m from the rocks, and were completed on foot.

Between January 1991 and August 1996, seals beached (dead) or injured along the coast were examined for shark bite wounds. Old Port Elizabeth Oceanarium (PEO) stranding log books (1987–1991) were examined for additional records of shark bitten seals.

Comprehensive information was collected from seals with fresh bite wounds, and old scars that resembled shark bites. Wounded animals were classified as pups, juveniles (7 months to 2 years) and subadult/adults (≥ 3 years of age). Bite position was classified as upper body (head and neck region); mid-body (shoulder, chest, fore-flippers); lower body (from posterior to the fore-flippers); and hind-flippers.

A fresh shark bite wound was defined as pink or bloody in appearance, or showing little evidence of having healed (Ainley *et al.*, 1985). Fresh bites were classified as: (a) shallow/deep punctures; (b) shallow/deep lacerations; (c) open wounds on the body; and (d) dismemberment (amputation of limbs; decapitation; body severed) (Fig. 14(a).2). Punctures, lacerations and open wounds were usually semi-oval or oval in shape (Le Boeuf *et al.*, 1982; Randall *et al.*,

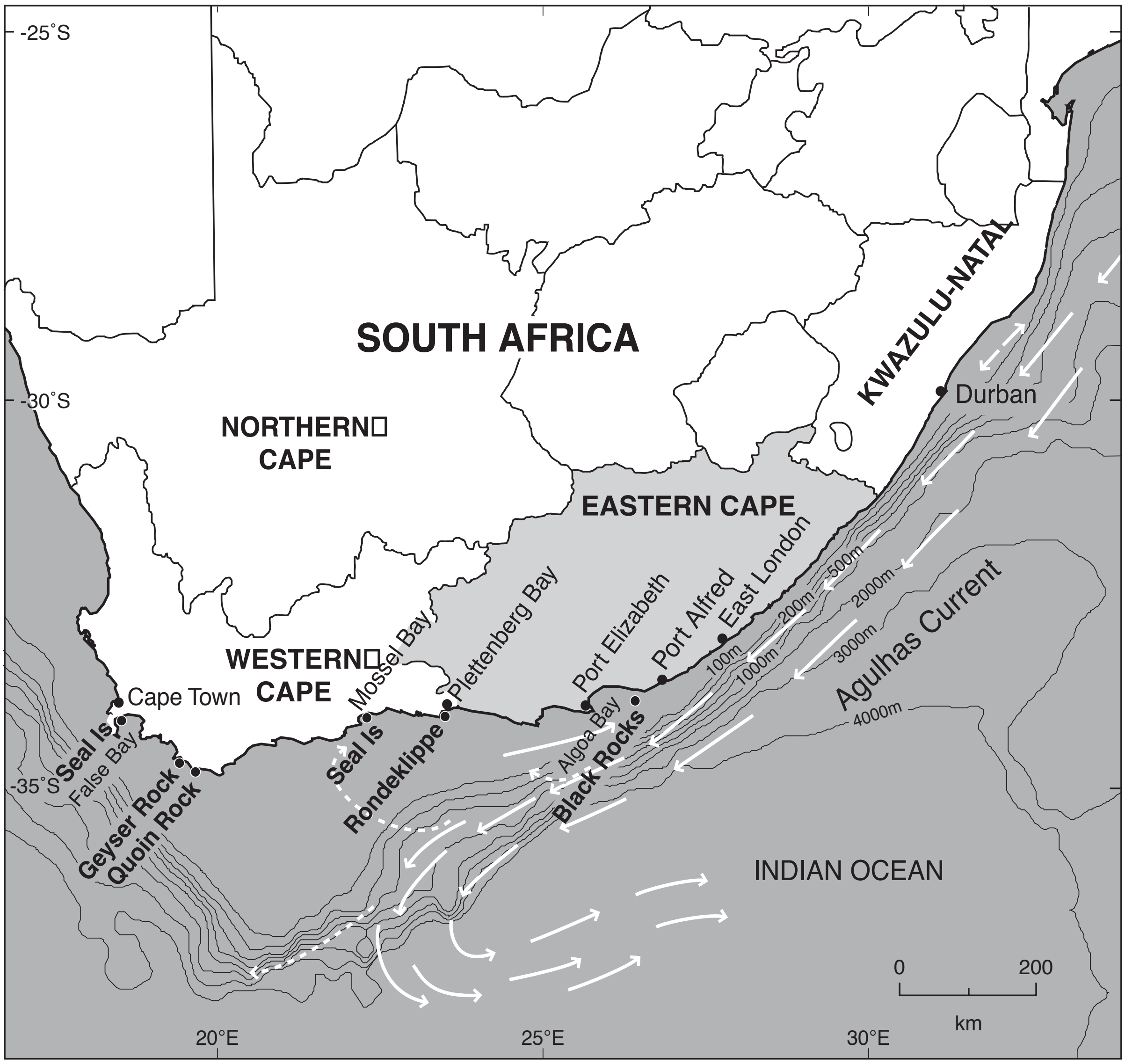

Fig. 14(a).1 Study area showing the locations of Black Rocks (Algoa Bay) and Rondeklippe (Plettenberg Bay) seal colonies off the Eastern Cape coast of South Africa.

1988; Long & Jones, 1996; Long *et al.,* 1996). Shallow wounds penetrated the skin and/or blubber, whereas deep wounds exposed the underlying muscle and/or bone.

To determine the percentage of shark bitten animals at the two seal colonies ground counts of wounded seals were conducted during the breeding season, when the number of animals was maximal. These took place at Black Rocks on 16 November 1993, and at Rondeklippe on 6 December 1994. Only fresh wounds were counted.

The total number of seals at Black Rocks was estimated from near vertical aerial photographs taken 24 December 1993, through the open door of a Cessna 172, flying at a speed of 60 knots and an altitude of 300–350 feet. Black and white photographs were enlarged (25 × 20 cm) and the number of black pups counted by two readers using a magnifying lamp. The estimated minimum number of pups (i.e., the number of individual pups counted by both readers + additional pups counted by reader one and reader two) was then multiplied by five to obtain an estimate of the total population (Anonymous, 1991).

Unpublished records of shark bitten subantarctic fur seals, *Arctocephalus tropicalis*, found beached or injured along the south-east coast were also included in this study. These records were collected over a 15 year period, between July 1979 and August 1994 (Stewardson *et al.,* unpubl. data). Fresh shark bite wounds and old scars that resembled shark bites were noted. These records were used for comparative purposes, to assess attack behaviour inferred from the position of wounds on the seal's body.

RESULTS

Observations of shark attacks on live Cape fur seals indicated that: (i) large white sharks prey on Cape fur seals in Eastern Cape waters; (ii) pups, juveniles and adults are taken; (iii) the seals were attacked from

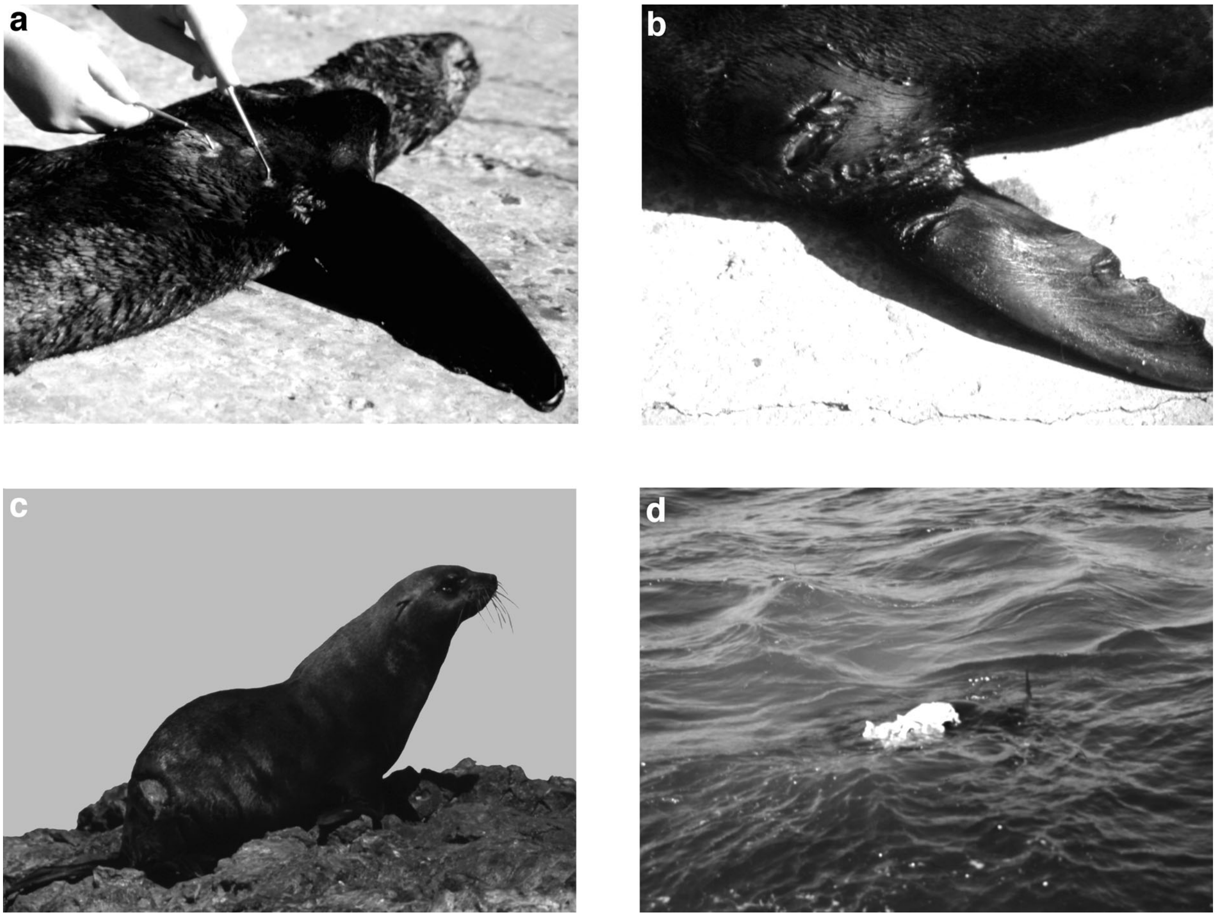

Fig. 14(a).2 Shark bite wounds observed on Cape fur seals from the Eastern Cape coast of South Africa: (a) punctures, (b) lacerations, (c) open wounds on the body and (d) dismemberment.

behind; and (iv) the sharks fed immediately (Table 14(a).1). Shortfin mako sharks (1–4 m in length) and blue sharks, *Prionace glauca*, have been observed pursuing seals (juveniles and large adult males) in this region; however, no kills have been confirmed (Dave Craig, pers. comm.).

During six day trips to Black Rocks colony, a total of 13 seals with fresh shark bite wounds were identified; all were adults (Table 14(a).2). The ratio of injured males to females was 1 : 3. These animals had been bitten only once before escaping. Sixty nine percent of wounds were located on the lower body.

Table 14(a).1 *Eyewitness accounts of white sharks killing and consuming Cape fur seals on the Eastern Cape coast of South Africa*

No.	Date	Location	Total length of shark (m)	Age class of seal	Description of attack	Witness
1	Jan/Feb 1992	Rock River (Nature's Valley)	*c.* 4	Adult	- seal was attacked from the rear - whole seal consumed - bite sequence NR	B. Joubert
2	Jan 1993	Robberg (Plettenberg Bay)	*c.* 3	Juvenile	- seal was attacked from the rear - whole seal consumed in a single bite	W. Stanley
3	NR	Bird Island (Algoa Bay)	*c.* 4	Black pup	- seal was attacked from the rear - hind-flippers severed first - whole seal was consumed	Anon (Bird Island guano worker)

NR, not recorded.

Table 14(a).2 ***Fresh shark bite wounds and bite scars found on Cape fur seals sighted at Black Rocks seal colony between May 1992 and November 1994***

No.	Date	Locality	Age class	Sex	Bite category[a]	No. of bites	Bite position[b]	Other comments
1	11 May 1992	Black Rocks	Adult	M	fresh open wound	1	lower body (dorsal)	Infected wound & locomotion impaired
2	11 May 1992	Black Rocks	Adult	F	fresh deep laceration	1	mid-body (dorsal)	–
3	11 May 1992	Black Rocks	Adult	F	fresh open wound	1	mid-body (fore-flipper)	–
4	11 May 1992	Black Rocks	Adult	F	fresh deep laceration	1	hind-flipper	–
5	11 May 1992	Black Rocks	Adult	F	fresh superficial laceration	1	lower body (dorsal)	–
6	16 November 1993	Black Rocks	Adult	F	old bite (healed)	1	lower body (dorsal)	–
7	16 November 1993	Black Rocks	Adult	F	fresh open wound	1	hind-flipper	Infected wound
8	16 November 1993	Black Rocks	Adult	F	fresh open wound	1	lower body (dorsal)	Pregnant (full term)
9	16 November 1993	Black Rocks	Adult	M	old bite (healed)	1	lower body (dorsal)	Bull in breeding condition
10	16 November 1993	Black Rocks	Adult	M	fresh superficial laceration	1	lower body (dorsal)	–
11	16 November 1993	Black Rocks	Adult	M	old bites (partially healed)	2	lower body (dorsal) mid-body (ventral)	–
12	20 November 1993	Black Rocks	Adult	M	fresh deep laceration	1	lower body (dorsal)	Bull in breeding condition
13	20 November 1993	Black Rocks	Adult	F	fresh deep laceration	1	lower body (dorsal)	Pregnant (full term)
14	22 February 1994	Black Rocks	Adult	F	fresh open wound	1	lower body (dorsal)	Observed feeding pup
15	22 February 1994	Black Rocks	Adult	F	old bites (healed)	2	lower body (dorsal)	Poor physical condition
16	22 February 1994	Black Rocks	Adult	M	old bites (healed)	2	lower body (dorsal)	Bites slightly overlapping
17	15 September 1994	Black Rocks	Adult	F	fresh open wound	1	lower body (dorsal)	–
18	27 October 1994	Black Rocks	Adult	–	fresh dismemberment	–	lower body (axillary girth)	Lower body floating at water surface
*19	5 December 1994	Rondeklippe	Adult	M	old bite (healed)	1	mid-body (fore-flippers & chest)	Large bull, (TL *c.* 2.2 m)
*20	5 December 1994	Rondeklippe	Juvenile	–	fresh superficial laceration	1	mid-body (fore-flippers)	Poor physical condition & locomotion impaired

[a] See text, page 296.
[b] See text, page 296.
* Seals 19 and 20 from Rondeklippe; observations made during the breeding season.

Few animals had wounds to the hind-flippers (two seals) or mid-body (two seals). No head or neck wounds were observed. Two animals had infected wounds, one had difficulty in walking, and one dead animal was presumably killed during the attack.

Old scars resembling shark bite wounds were found on five animals; two adult females and three adult males (Table 14(a).2). On most, bite scars were on the lower body. Three animals had more than one bite scar.

From January 1991 to December 1995, a total of 114 Cape fur seals were found beached (dead), or drowned in commercial trawl nets. Four of these seals (3.5%) had fresh shark bite wounds: three juveniles and one adult (Table 14(a).3). Each animal had a single shark bite located on the lower or mid-body. No head or neck wounds were observed. Two animals were in poor body condition, and one live animal had a dislocated shoulder and was in shock. Macroscopic visual observation of gross body organs did not disclose obvious abnormalities.

Table 14(a).3 *Fresh shark bite wounds and bite scars found on Cape fur seals beached (dead), or drowned in commercial trawl nets, between January 1991 and December 1995*

No.	Date ashore	Locality	Dead or Alive	Age class	Sex	SBL[a] (cm)	Weight (kg)	Bite category[b]	No. of bites	Bite position[c]	Bite width (cm)	Other comments	Accession no.[d]
21	11 March 1993	Pollock Beach (Port Elizabeth) 33°59'S, 25°41'E	D	Juvenile	M	118	23	fresh open wound	1	lower body (dorsal)	20	–	PEM2035
22	28 May 1993	Seaview (Port Elizabeth) 34°02'S, 25°31'E	D	Adult	M	206	–	old bite (healed)	1	lower body (dorsal)	–	–	PEM2044
23	28 June 1993	Trawl net 34°43'S, 24°28'E	D	Adult	M	171	–	old bite (healed)	1	hind-flipper	21	–	PEM2052
24	5 July 1994	Schoenmakerskop 34°02'S, 25°33'E	D	Juvenile	M	103	15	fresh deep punctures	1	mid-body & lower body (ventral & dorsal)	19	Poor physical condition	PEM2201
25	23 July 1994	Maitlands 33°59'S, 25°18'E	A[e]	Juvenile	F	86	12	fresh deep punctures	1	mid-body (ventral)	23	Fractured shoulder & shock	PEM2204
26	27 August 1995	Seaview 34°01'S, 25°27'E	D	Adult	M	130	–	fresh deep laceration	1	lower body (dorsal)	12	Poor physical condition	PEM2415

[a] Standard body length (straight line from tip of the snout to tip of the tail, with the animal lying on its back).
[b] See text, page 296.
[c] See text, page 296.
[d] Port Elizabeth Museum accession number.
[e] Alive, but died within hours of collection.

Old scars resembling shark bite wounds were found on two adult males (Table 14(a).3). Each animal had a single bite scar, located on the lower body or hind-flippers.

From January 1987 to September 1991, a minimum of seven Cape fur seals were treated for shark bite wounds at the Port Elizabeth Oceanarium: one pup, three juveniles, and three adults (Table 14(a).4). Four of these animals were males; three were unsexed. Eighty six percent of wounds were located on the lower body or hind-flippers. Only one animal had wounds to the mid-body. No head or neck wounds were observed. It was not possible to calculate a percentage for shark bitten seals because the total number of seals treated at the oceanarium during this period was not recorded.

The total population estimate for the 1993 breeding season at Black Rocks was 915 animals (i.e., 183 pups). On 16 November 1993 a minimum of three animals had fresh shark bite wounds; 0.3% of the animals examined (Table 14(a).2).

The total population estimate for the 1994 breeding season at Rondeklippe was 11 animals. On 5 December 1994, fresh shark bite wounds were observed on one of these animals; (Table 14(a).2).

From July 1979 to August 1994, a total of 158 subantarctic fur seals were recorded in the study area, of which nine (5.7%) had fresh shark bite wounds (Table 14(a).5). Twenty six animals returned to sea soon after their arrival; 17 were beached (dead), and 115 were taken to the local oceanaria for rehabilitation, or were relocated. Many of the emaciated animals died during rehabilitation. The majority of bite wounds were found on the mid-body and lower body. No head or neck wounds were observed. Three animals had infected wounds (seals 5, 8 and 9), two of which died from septicaemia.

Table 14(a).4 ***Fresh shark bite wounds and bite scars found on injured Cape fur seals brought into the Port Elizabeth Oceanarium for medical treatment between January 1987 and September 1991***

No.	Date ashore	Locality	Age class	Sex	Bite position[a]
27	2 May 1987	Jeffrey's Bay 27°34'S, 32°41'E	Black pup	–	mid-body (fore-flipper)
28	1 December 1988	Swartkops Beach 33°52'S, 25°38'E	Juvenile	–	hind-flippers
29	8 December 1991	Maitlands 33°58'S, 25°17'E	Juvenile	M	lower body (dorsal)
30	14 May 1994	–	Adult	M	hind-flippers
31	5 July 1994	Schoenmakerskop (Port Elizabeth) 34°02'S, 25°33'E	Adult	M	lower body (dorsal)
32	19 June 1996	Cape Recife 34°01'S, 25°42'E	Juvenile	–	lower body (dorsal)
33[b]	2 August 1996	East coast-offshore (Trawl net)	Adult	M	lower body (dorsal & ventral) & hind-flippers

[a] See text, page 296.
[b] The lower back of animal 33 was partially paralysed from the bite (captured alive in trawl net).

DISCUSSION

Predatory sharks

In Eastern Cape waters only the white shark and broadnose sevengill sharks are known to actively feed on live Cape fur seals (Cliff *et al.*, 1989, 1996; Ebert, 1991 *a*, *b*; M. Smale, pers. comm.; present study). Bluntnose sixgill sharks feed on Cape fur seals; however, it has yet to be confirmed if live prey or carrion is taken (Ebert, 1994; M. Smale, pers. comm.).

Several factors suggest that white sharks are responsible for the majority of attacks on Cape fur seals from the Eastern Cape coast: (i) white sharks have been observed attacking and eating Cape fur seals in this area (present study); (ii) seal remains have been found in the stomachs of white sharks captured along the south-east coast (Cliff *et al.,* 1989, 1996; D. Craig, pers. comm.); (iii) there have been numerous reports of large sharks (300–550 cm) near the Eastern Cape seals colonies (Ferreira & Ferreira, 1996); (iv) Black Rocks is thought to be a pupping ground for white sharks, as suggested by the large number of small sharks (*c.* 180 cm) found there (Cliff *et al.,* 1996; Ferreira & Ferreira, 1996); (v) white sharks inflict large bites (10–50 cm) resembling ovate or crescentic arcs with triangular punctures or jagged tears (Long *et. al*, 1996), typical of those found on dead and injured seals (present study).

Shark bites

A total of 33 Cape fur seals was observed with shark bite wounds (25 seals with fresh bites; eight seals with shark bite scars). Injuries included punctures, lacerations, open wounds and dismemberment. Bite width measured on dead animals ranged from 12–23 cm, indicating that these animals were attacked by large sharks (Long & Jones, 1996). Some injured animals showed signs of impaired body movement (four seals), and infection (two seals).

Age of prey

Shark inflicted injuries were observed on one pup, seven juveniles and 25 adults. The large number of adults with shark bite wounds suggests that either: (i) adults are attacked more often than young animals, or (ii) predatory attacks on adult seals are less successful than attacks on younger seals. Young seals may be more vulnerable to shark attack because of their smaller, manageable size, undeveloped swimming/diving abilities, and their inexperience (Le Boeuf *et al.,* 1982; Brodie & Beck, 1983; Ainley *et al.,* 1985; Le Boeuf & Crocker, 1996). Therefore, it is likely that the low incidence of shark bite wounds observed on young Cape fur seals indicates that such attacks are usually fatal (Brodie & Beck, 1983; Hiruki *et al.,* 1993; present study). Large body size of adult seals (males: mean range 200–300 kg; females: mean range 40–80 kg; David, 1987) would increase their chance of surviving an attack, whereas younger animals are more likely to succumb.

Location of bites

Fur seals (Cape and subantarctic) with single shark bite wounds, were usually bitten on the lower body, suggesting that animals were approached from behind. Larger sharks presumably find it difficult to capture fleeing otariids; therefore, they usually attack from behind and/or below unsuspecting animals, at or near the water surface (Tricas & McCosker, 1984; Tricas, 1985; Klimley *et al.,* 1996; Long *et al.,* 1996). Once bitten, white sharks usually release their prey for a short period before feeding (Klimley *et al.,* 1996). By releasing the injured seal immediately after the initial strike, the predatory shark presumably reduces the risk of injury from the seal's highly developed fore-flippers, sharp teeth and nails (Tricas & McCosker, 1984; McCosker, 1985; Tricas, 1985; Klimley *et al.,* 1996). Because the fore-flippers are not usually disabled during the initial strike, large otariids may escape before the second strike. Unlike phocids, which use hind-flipper locomotion, otariids propel themselves through the water with their fore-flippers. If the hind-flippers of the otariid are damaged during the initial strike, the animal still retains mobility, whereas phocids generally surface immobile (Ainley *et al.,* 1985; Klimley *et al.,* 1996).

Seasonality

In the present study, coastal PEM/PEO records indicate that 77% of shark bitten Cape fur seals were observed in May–August (Austral autumn/winter). This may reflect an increase in shark abundance in the area. At Dyer Island and Struis Bay (Western Cape), white sharks are present throughout the year, with peak sightings in July/August (Ferreira & Ferreira, 1996). In the warmer waters of KwaZulu-Natal, shark numbers appear to peak from August to January (Cliff *et al.,* 1996). If white sharks are more abundant near the Eastern Cape seal colonies in autumn/winter, then younger seals and/or nursing cows would be their main prey because young seals remain close to the colony, but make brief trips to sea to supplement their milk diet with fish and crustacea (Rand, 1956). In contrast, seals > 2 years of age, including non-nursing cows, spend much of their time at sea feeding during this period (Rand, 1956).

Percentage of seals with shark bite wounds

Fresh shark bite wounds were found on a minimum of 3.4% of Cape fur seals found stranded on local beaches, and 0.3% of seals observed at the Black Rocks colony during the breeding season. However, these estimates do not account for the number of fatal attacks, and, therefore, underestimate the extent of shark-seal interactions in this area. Furthermore, when estimating the number of wounded animals from coastal strandings, several factors may bias counts negatively. For example: (i) currents and tides may prevent seals from washing ashore, or carry beached animals out to sea; (ii) some dead seals may sink to the ocean floor, or be scavenged by other animals; (iii) strandings may occur in sparsely populated or in less accessible areas, and are less likely to be reported; and (iv) it is not always possible to differentiate between direct predation and post-mortem scavenging. When counts are conducted at the colonies, estimates may also be negatively biased because: (i) it is not possible to see the ventral surface of all animals; (ii) animals partially submerged at the waters edge, or feeding at sea, are excluded from counts; (iii) superficial wounds are possibly overlooked, hidden beneath the seal's thick pelage.

CONCLUSIONS

The data presented in this study provides the first published records of shark inflicted injuries on southern fur seals *Arctocephalus* spp. south of 10°S. Preliminary findings suggest that white sharks are responsible for the majority of attacks on Cape fur seals from the Eastern Cape coast. Although predatory encounters appear to be common, long term studies are required before we can fully assess the extent of shark predation in this area. Such research should include quantitative data on: shark prevalence, length, diets and feeding behaviour; identification of species of sharks responsible for fresh bite wounds found on the bodies of dead or injured seals; and regular observations at the East Cape colonies to assess the seasonal and inter-annual extent and effects of shark predation.

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Appendix 14(a).5 ***Fresh shark bite wounds found on vagrant subantarctic fur seals collected from the south-east coast of southern Africa between July 1979 and August 1994***

No.	Date ashore	Locality	Age class	Sex	Bite position[a]	Other comments
1	9 October 1984	Port Alfred 33°36'S, 26°55'E	Adult	M	–	poor physical condition; died (13 October 1984); PEM1085
2	19 June 1986	Flat Rocks (Port Elizabeth) 34°00'S, 25°42'E	Adult	M	lower body (dorsal)	poor physical condition; returned to sea (22 June 1986)
3	17 August 1987	Shelly Beach (Durban) 30°48'S, 30°25'E	Adult	M	lower body (dorsal)	released (16 March 1988); *A. tropicalis/gazella* hybrid; named Rattigan
4	15 July 1988	Sodwana Bay 27°34'S, 32°41'E	Juvenile	F	mid-body (dorsal) & hind-flippers	mid-body wound required 30 stitches; sold (10 October 1989) to WMSP, England; named Otta
5	26 July 1988	Beach View (Port Elizabeth) 34°00'S, 25°49'E	Juvenile	F	mid-body (fore-flipper) & lower body (dorsal)	wound infected/ maggots; resident of PEO; named Tess
6	26 July 1989	Humewood (Port Elizabeth) 33°58'S, 25°38'E	Adult	M	mid-body (fore-flipper)	poor physical condition; returned to sea (26 July 1989)
7	15 July 1989	Schoenmakerskop (Port Elizabeth) 34°02'S, 25°33'E	Adult	M	–	poor physical condition; released (22 July 1989); found dead at Bird Island (25 July 1989) with fresh shark bite wounds
8	2 September 1990	St Lucia 28°24'S, 32°26'E	Juvenile	_	_	developed septicaemia; died (6 September 1990); named Aero
9	30 August 1991	Virginia Beach (Durban) 29°46'S, 31°04'E	Adult	M	lower body (dorsal)	developed septicaemia; died (31 August 1991); named Tim

[a] See text, page 296.

PEO, Port Elizabeth Oceanarium.

WMSP, West Midlands Safari Park, England.

CHAPTER 14(b)

Supplementary paper

Aggressive behaviour of an adult male Cape fur seal (*Arctocephalus pusillus pusillus*) towards a great white shark (*Carcharodon carcharias*)

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This is a report of a marine predator (the white shark) being threatened by a member of the species on which it preys (a male Cape fur seal). Although these events may be rarely observed or occur infrequently, they may have important implications for the predator and its prey. We suggest that shark mobbing by adult male Cape fur seals is adaptive for the reduction of risk of predation by sharks. Mobbing of sharks is likely to alert conspecifics to the presence of a predator, and/or reduce the shark's hunting motivation near the mobbing site.

Key words: Arctocephalus pusillus pusillus, Carcharodon carcharias, predator, mobbing

Aggressive behaviour of an adult male Cape fur seal (*Arctocephalus pusillus pusillus*) towards a medium-large great white shark (*Carcharodon carcharias*) was observed on 7 December 1994 at the Robberg Nature and Marine Reserve, Plettenberg Bay, on the south east coast of South Africa (34°03'S; 23°24'E). Observations were made from a cliff face about 6 m directly above the Rondeklippe fur seal colony, which at the time comprised 11 animals: eight adult males, one subadult male, one adult female and one unsexed juvenile.

At 10:47 on 7 December 1994, we sighted a 3.5–4.0 m great white shark, just beneath the water surface, about 8 m northwest of the seal colony. The shark moved steadily towards the cliff line, and then veered eastward towards the colony where nine resident seals were lying on the rocks. The dominant[1] male and another adult male were at sea and had not been sighted since their departure earlier that morning (08:49).

As the shark approached to within several metres of the main landing-area, the dominant male seal, estimated to be at least 2 m in length and 300 kg in weight, suddenly appeared. The seal turned to face the shark, and swam directly towards the intruder in a threatening charge, forcing the shark to divert in a northeasterly direction. The charge was continuous, orientated and at the water surface (Fig. 14(b).1). No direct contact was made. The attacking fur seal then chased the shark at a distance of less than a body length until it was at least 15 m from the colony. At no time during the encounter did the shark show obvious signs of aggression. The dominant male returned to the colony but remained in the water; he appeared calm, occasionally rolling in a 360° lateral turn, presumably keeping a look-out for ascending sharks (see McCosker 1985). At 10:54 he hauled out onto the rocks and joined the other seals.

At 11:14, the same male accompanied six of the seals (five males and the female) into the water, and they departed as a pod in a westerly direction. This gregarious behaviour may be at least partly associated with predator avoidance, i.e., if a shark were sighted by at least one of the seven seals then the entire pod would be alerted (Ainley *et al.*, 1985; McCosker 1985).

Similar attacks on large sharks have been reported in other species of pinnipeds, otariids and phocids, e.g., Galàpagos sea lions (*Zalophus californianus*), Galàpagos fur seals (*Arctocephalus galapagoensis*) and Hawaiian monk seals (*Monachus schauinslandi*) (Nelson 1968; Barlow 1972, 1974; Alcorn & Kam 1986: Johanos & Kam 1986; Trillmich 1996). Although these events may be rarely observed or occur infrequently, they may have important implications for the predator and its prey. It is not known why seals attack sharks; however several possibilities are suggested below.

Aggressive tendencies during the breeding season

The Cape fur seal breeding season extends from late October to late December, and during this time large breeding males exhibit aggressive territorial maintenance behaviour and fight for control of harems (Rand 1967). Vocal threats and threatening charges are commonly observed at the breeding rookeries. This change in male behaviour appears to be associated with functional gonads and their products, androgens (Bester 1990; Stewardson *et al.*, 1998). Large males show aggression on land and in stretches of water adjoining the rookeries. Narrow inlets and channels near the main landing-areas are often subdivided among breeding males; these 'aquatic territories' are vigorously defended (Rand 1967). It is likely that breeding males will attack any object that roughly resembles an intruding rival male (Miller 1974), including large sharks.

If adult male Cape fur seals were shown to attack only during the breeding season, then high androgen levels might partially explain our observation. However, Trillmich (1996) described mobbing behaviour of sharks by male, female and juvenile Galàpagos sea lions and Galàpagos fur seals, indicating that high androgen levels are not necessary for aggressive behaviour to be exhibited towards large sharks.

Paternal role

Barlow (1972) found that large Galàpagos sharks (*Carcharhinus galapagensis*), which swim near the territories of breeding male Galàpagos sea lions, are usually chased away by one or several adult males ('mobbers'). The adult males appear to protect the young seals by escorting the sharks away, i.e., the pups dash shoreward as the shark is being intercepted. This may be interpreted as paternal behaviour of territorial males, which promotes the survival of related pups and hence improves the inclusive fitness of the males (Barlow 1972, 1974; but see Miller 1974). The argument is proposed that a bull is likely to be protecting his genetic investment by repelling sharks from anywhere around the rookery,

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[1] For the purpose of this report, the term 'dominant' is used loosely to describe the rank of one of the two largest male seals [i.e., Rondeklippe seals were submissive to this male; a large non-resident male seal feeding near the colony was attacked (frontal-strike) and chased by this male (Stewardson. pers.obs.)].

Fig. 14(b).1 A marine predator (the white shark) being threatened by a member of the species on which it preys (a male Cape fur seal).

Top: at 08:49, 7 December 1994, the dominant male seal in the group departs from the colony. (Note the very large body size of the dominant male compared to the two adult males at the water's edge. There is an old shark-bite wound across the chest and foreflippers of the dominant male indicating previous encounters with sharks).

Middle: at 10:48, a medium-large great white shark, about 3.5–4.0 m in length approaches the Rondeklippe seal colony.

Bottom: as the shark approaches to within several metres of the main landing-area, the dominant male suddenly appears and swims directly towards the shark in a threatening charge. The intruding shark was forced to divert from the oncoming seal, and was chased in a northeastly direction, about 15 m from the fur seal colony.

(The images were taken from video footage).

because pups carrying his genes may move about through any territory (Barlow, 1974).

However, in the present study, mobbing of the shark by the dominant male did not have a paternal role. At the time Rondeklippe was a non-breeding colony. There were no pups at the colony when the attack occurred.

Mobbing of predators

Studies suggest that mobbing of predators may benefit the 'mobber' and conspecifics, including the blood relatives of the 'mobber' (Kobayashi 1994). For example: (1) the mobber may acquire information about a predator, and relay this information to conspecifics, alerting them to potential danger (i.e., mobbing has a signal effect, alerting conspecifics of the presence of a predator, thus reducing the likelihood of predation); (2) mobbing behaviour threatens and/or confuses the predator, which may reduce the predator's hunting effectiveness and motivation near the mobbing site; (3) mobbing may make other conspecifics who have no innate recognition of the predator know that the mobbed animal is dangerous (Curio *et al*., 1978).

Trillmich (1996) found that shark mobbing by male Galàpagos sea lions and male Galàpagos fur seals presumably serves to move sharks away from preferred seal resting places, or to chase them from feeding sites. Because territorial males are more prone to shark predation (e.g., spend more time at the water's edge), males can benefit greatly from mobbing if mobbing keeps sharks away (Trillmich 1996).

Based on limited observational data, we suggest that aggressive behaviour of adult male Cape fur seals towards large white sharks is adaptive for the reduction of the risk of shark predation. This behaviour is likely to alert conspecifics to the presence of a predator, and/or reduce the shark's hunting motivation near the mobbing site. Further studies are required to determine the prevalence of mobbing of sharks by Cape fur seals, and to investigate the benefits and risks of mobbing behaviour. Depending on the 'motivational state' of the shark, mobbing may be an option or not: fleeing may be more adaptive if the shark does not retreat, i.e., the mobber may be bitten or even killed (L. Compagno. pers. obs.).

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CHAPTER 15

Conclusions and future directions

CONCLUSIONS

In this multi-disciplinary study, I have documented the general biology of the Cape fur seal, including various aspects of anatomy, age and growth, sexual dimorphism, reproduction, parasitology, diet and foraging, and population size. Such information is of fundamental importance when formulating a meaningful seal conservation and management policy for the Eastern Cape coast.

Secondly, by examining historical records, I was able to document changes in the distribution and abundance of the local seal population. It was evident that seals in this region were almost exterminated due to excessive exploitation during the 1800s to the mid 1900s. Seven of the eight original seal colonies were extirpated. By destroying seal herds through indiscriminate practices, and confining the population to Black Rocks, the population has been unable to build up its numbers sufficiently to stimulate colonisation on neighbouring islands. Limited space for breeding seals on Black Rocks, and the influence of storms restricts the number of pups that can be reared successfully. It is therefore unlikely that the Black Rocks population can increase quickly enough to flow onto Seal and Stag Island, without being depleted by storms.

Thirdly, I have identified immediate and potential threats to the local seal population. Immediate threats include deliberate shooting of seals; incidental catch in commercial fishing gear; and storms (gale force winds and high swells) during the pupping/mating season. Entanglement in man made debris was identified as a potential threat. Other potential threats, not examined in the present study, include disturbance, habitat degradation, and episodic mass mortalities.

Threats

Deliberate shooting of seals

Although Cape fur seals are protected under Section 3(b) of the Sea Birds and Seals Protection Act 46 (1973), at least 1 000 seals are shot in Eastern Cape waters annually. At sea, it is not always possible to achieve a clean head shot, therefore, many seals are shot in the stomach or back, and die a slow, painful death.

Incidental catch in commercial fishing gear

In Eastern Cape waters, the annual overall mortality rate of Cape fur seals drowned in nets and deliberately killed during commercial trawling operations was estimated to be 549 (0.142 per trawl). Drowned animals were predominantly males, ≥ 5 y. Although the local seal population remains viable, the long term effects of changing the population structure, by removing males ≥ 5 years, are unknown.

Entanglement

Entanglement of Cape fur seals in man made debris such mono-filament line, trawl net fragments and rope, did not appear to impact significantly on the local seal population. Observations during the 1993 pupping season at Black Rocks indicated that the minimum estimated frequency of entanglement was *c*. 0.11–0.22%. However, as the fishing industry continues to expand, more synthetic material will accumulate, and the incidence of entanglement in this area will subsequently increase.

Furthermore, as tourism increases, problems associated with ocean and beach litter (plastic bags, fishing line, nets and other rubbish) become more widespread. Land litter from catchments and stormwater drains is a major source of ocean and beach litter.

Disturbance caused by human activity

Blacks Rocks seal colony is relatively remote from human activity, i.e. 8–9 km offshore. However, the Rondeklippe colony, which is situated on the mainland, is in a popular tourist area. As recreational boating activities and tourism increases, seals may alter their behaviour and habitat use to avoid contact with humans.

Furthermore, the Coega Development Corporation is planning to build an industrial zone and a harbour at Coega (near Port Elizabeth). This site is *c.* 63 km from Black Rocks and overlaps with the seals foraging range. It is likely that the development will have serious negative affects on Cape fur seals and other marine life in the area. For example, there is the risk of pollution from toxic waste generated by the industries; and disturbance from underwater sound caused by dredging, harbour construction and increased shipping activities.

Habitat degradation

Oil spills pose a potential threat to seals in Eastern Cape waters. Ingestion of toxic hydrocarbons; absorption of oil into the fur, skin and mucous membranes; and loss of habitat, can adversely effect individual seals. The potential of an oil spill from fuelling ships in the port, operational discharges from shipping, and shipping accidents will increase if controversial plans to construct an industrial zone and a harbour, by the Coega Development Corporation, are realised.

Episodic mass mortalities

Considering that the seal population in Eastern Cape waters is small, an outbreak of disease would be potentially disastrous. The following examples demonstrate the potential vulnerability of pinnipeds to disease epidemics: (i) in 1964, uncinariasis was identified as the primary cause of death in northern fur seals (*Callorhinus ursinus*) at St Paul Island in the Pribilofs, Alaska (Keyes, 1965); (ii) in 1970, an outbreak of Leptospirosis in California sea lions (*Zalophus californianus*) along the California and Oregon coasts affected hundreds of adult males, and was thought to be associated with a high rate of abortion in females (Vedros *et al*., 1971; Smith *et al.,* 1974); (iii) in 1979 to 1980, more than 400 harbour seals (*Phoca vitulina*), mostly juveniles, died in New England from acute pneumonia associated with the influenza A virus (Reeves *et al.,* 1992); (iv) 20% of California sea lions pups died at San Miquel Island following premature parturition caused by an outbreak of the San Miquel sea lion virus (a calicivirus) (Gilmartin, *et al.,* 1976); and (v) in 1988, an outbreak of Phocine distemper virus (a morbillivirus) in the North Sea severely reduced several populations of harbour seals (Osterhaus & Vedder, 1988); and also reduced the grey seal (*Halichoerus grypus*) population, were pup production fell by 20% (Reeves *et al.,* 1992).

FUTURE RESEARCH

Monitoring seal numbers

In order to conserve and manage Cape fur seals in Eastern Cape waters, research should concentrate on monitoring seal numbers.

Considering that a large number of seals are being shot and entrapped in commercial trawl nets, continuing monitoring of the local population is essential. Aerial photography should continue to be used to count the number of pups present during the peak pupping period (usually the third week in December). The number of pups should be multiplied by five to give an estimate of the total population. Counts should be conducted each year. However, it is important to note that it is difficult to take good quality aerial photographs of pups on Black Rocks (i.e., black pups against a dark background), and estimates using this method are negatively biased. The use of tag-recapture methods is not to be recommended at this small island colony. When tagging pups at this site there is considerable disturbance, e.g., pups can be trampled or washed out to sea. Occasional ‘ground truthing’ of aerial counts is recommended. This can be achieved with a maximum of two observers conducting counts, using binoculars, from several vantage points. Traversing the entire rookery during the breeding season is not recommended.

Minimising negative interactions between seals and fishermen

In order to prevent seals interfering with fishing operations, and becoming entrapped in commercial trawl nets, research is needed to develop affordable, efficient and humane methods of deterring seals from fishing gear or fishing areas. Considering that 1 or 2 seals can cause losses for fishermen, culling is unlikely to reduce the magnitude of losses appreciably. Seal deterrents need to be developed for trawl nets, line fish vessels and squid jig vessels. Methods of deterring seals already tested include: (i) various types of explosive fire-crackers (e.g., Thunderflashes, Belugas, and Seal deterrent) (Anon, 1976; Shaughnessy *et al.,* 1981); (ii) electric pulses and air guns (Anon, 1977); (iii) recorded sounds of killer whales, crackers and sounds of shots fired into the water (Anon. 1975*a*; Anon1975*b*; Anon 1978; Shaughnessy *et al.,* 1981); and (iv) an electronic unit called a Seal Scram which emits random underwater sound pulses set at a certain frequency (Wickens *et al.,* 1992). Some of these methods are thought to frighten fish, and none have been consistently successful at deterring seals (Wickens *et al.,* 1992).

Discarding of whole/parts of fish encourages seals to follow vessels. Therefore, research into efficient utilisation of/or disposal of offal and by-catch should be addressed. For example, mincers have been used to mince by-catch before it is thrown overboard, making it inaccessible to the seals (Wickens, 1994).

Monitoring the population for signs of disease

Considering that the seal population in Eastern Cape waters is small, a monitoring program accessing the incidence of disease is recommended. This can be achieved by collecting and analysing serum and tissue from seals which have stranded, or drowned in commercial trawl nets.

MANAGEMENT

In order to conserve seals in Eastern Cape waters, a comprehensive seal conservation and management plan is required. This can be achieved through the formation of a government ‘advisory body’ comprised of seal and fish biologists; members of the commercial fishing industry; representatives of government and non-government conservation groups; representatives of animal welfare groups; a marine mammal veterinarian; representatives of the department of town and planning; and local ecotour operators. Immediate and potential threats to the local seal population should be discussed in detail, and the appropriate policies and actions formulated.

The following key points should be discussed when formulating a seal conservation and management plan for the region:

(i) Incidental catch in commercial fishing gear

In order to minimise the number of seals entrapped in commercial trawl nets, it is necessary to design and trial new seal deterrent methods which discourage seals from approaching trawl nets. Successful methods must then be promoted.

Secondly, the possibility of altering fishing methods needs to be discussed with trawl operators.

Considering that seals make comparatively few dives > 160 m, trawl nets should be: (i) deployed as quickly as possibly; (ii) held at depths > 160 m; and (iii) retrieve as quickly as possible when being hauled to the surface.

Furthermore, each vessel should be supplied with suitable equipment to capture and remove seals from the ship's factory area. Currently, seals which enter the factory area are usually killed to prevent potential injury to crew.

(ii) Deliberate shooting of seals

Legislation should be introduced to prohibit firearms aboard commercial and recreational fishing vessels, thereby preventing large numbers of seals from being shot at sea and injured.

In order to discourage seals from damaging gear, taking fish from lines, and scattering fish schools, it is necessary to trial new methods of deterring seals from fishing areas. The use of effective deterrents in both the teleost line and squid jig fisheries must then be promoted.

(iii) Entanglement

In order to reduce the quantity of rubbish discarded directly into the ocean by commercial and recreational fishermen (particularly fishing line, rope, string, packing straps and net fragments), stricter enforcement of regulations on disposal of garbage from vessels is required.

In order to decrease the amount of land litter entering the ocean, education programs to change public littering practices are required. Improved waste management by local authorities is also needed.

Ongoing monitoring of the incidence of entanglement at Black Rocks during the breeding season should continue.

(iv) Disturbance caused by human activity

Marine ecotourism is a fast growing industry. It is therefore necessary to regulate tourist and recreational activities near seal colonies to minimise adverse impacts on resident seals. Currently, disturbance by visitors is a potential problem on the mainland, at Rondeklippe seal colony.

Access to the Black Rocks seal colony should be limited to minimise disturbance, especially during the pupping/mating season.

(v) Habitat degradation

As industrial development, shipping and recreational boating activities continue to increase in the area, the potential of an oil spill also increases. Therefore, it is necessary to formulate a detailed contingency plan to deal with an oil spill near the Black Rock seal colony. The plan must provide specific response guidelines.

Urban and industrial run-off are also significant sources of oil entering the marine environment. Improved management practices by local authorities are required to minimise this problem.

(vi) Episodic mass mortalities

Stranded Cape fur seals which have been injured and suffer various illnesses are often rehabilitated at the local Oceanaria, e.g., at Port Elizabeth, East London and Durban. The possibility of disease transfer after release must be considered. In order to minimise the risk of disease at Black Rocks seals colony, it is necessary to formulate strict guide lines concerning the release of stranded seals (or captive seals) back into the wild population.

(vii) Education

Education is one of the most effective tools of management. Through education, we can increase public awareness of Cape fur seals and their conservation needs; and promote activities to prevent population decline on the south/east coast.

Information on Cape fur seal conservation can be distributed within the general community through education programs in schools and universities; workshops in community centers; exhibits at Museums and art galleries; displays and educational program at local Oceanaria; community consultation; literature, and the media (e.g., television, radio, the internet, newspapers and magazines).

(viii) Marine protected area

Currently, the establishment of a marine protected area within Algoa Bay is under consideration. The proposed marine protected area extends from the mouth of the Sundays River to beyond Cape Padrone, and seawards to include the Bird Island group and the St Croix Island group, covering 56 500 ha. It will form part of the proposed 'Greater Addo National Park'. Strong community and government support is needed for this proposal to reach fruition. The establishment of a marine protected area around Black Rocks seal colony will provide safe access to breeding and haul-out sites; and conserve feeding ground close to the colony.

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”Pinnipeds are conspicuous competitors with humans for food and space.
They are victims of our expanding and often insensitive use of the sea”.

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APPENDIX A

Supplementary report

Climate of the Bird Islands (Algoa Bay) South Africa

Unpublished report submitted to the Port Elizabeth Weather Office, Walmer, South Africa, July 2001.

INTRODUCTION

Algoa Bay is a large, crenulated embayment facing the south-west Indian Ocean on the south-east coast of South Africa (Goschen & Schumann, 1988). Cape Recife forms the western boundary of Algoa Bay and the less prominent Cape Padrone forms the eastern boundary, with the port installations and the city of Port Elizabeth in the western section. Large columns of fresh water flow offshore from the Swartkops, Coega and Sundays rivers. The bay is characterised by a narrow continental shelf area and the Agulhas Current (Schumann, 1987; Goschen & Schumann, 1988). The sea surface temperature (SST) of the Agulhas Current varies seasonally with a maximum of 26^{O}C in summer and 3–4^{O}C less in winter (Schumann, 1987). There is a gradual cooling (3^{o}C drop) of the surface waters of the Agulhas Current as it flows southwards (Schumann, 1987).

Westerly winds have a dominant influence over the inshore shelf areas throughout most of the year. However, in summer, strong easterly winds are dominant. Strong easterly winds induce upwelling of cold nutrient rich water (Beckley, 1983; Goschen, 1988; Goschen & Schumann, 1988; Schumann, Ross & Goschen, 1988). Surface flow is generally in the direction of the wind, parallel with the coast-line (Harris, 1978; Hunter, 1981). Large scale weather patterns are dominated by the eastward-moving anticyclones from the South Atlantic high-pressure cell (Hunter, 1987). Coastal lows have a marked influence on the coastal environment (Hunter, 1987).

There are two island groups in Algoa Bay: the Islets of St Croix (Jahleel and Brenton Islets; St Croix Island) and the Bird Islands (Bird, Stag and Seal Islands; Black Rocks). These islands support significant bird breeding colonies, notably the Cape penguin, *Spheniscus demersus*, Cape gannet, *Morus capensis*, and roseate tern, *Sterna dougallii*; and a breeding colony of South African (Cape) fur seals, *Arctocephalus pusillus pusillus*. The seals breed on Black Rocks which is the eastern most extreme of their breeding range, and the only breeding colony in the Eastern Cape.

Although climate data are collected daily at the Port Elizabeth Airport (33^{o} 59’S, 25^{o} 36’E; height 60 m), which is representative of the general climatic conditions of the Port Elizabeth coast-line, a unique micro-climate exists at the Bird Island complex due to its positioning. Bird Island (33^{o} 50.67’S, 26^{o} 17.34’E), the largest of the 4 outcrops, is situated 63 km from the Port Elizabeth Airport, and 8–9 km from the mainland.

In June 1992, a seal research program was established in the Eastern Cape to examine the biology and conservation of the Cape fur seal (WWF project ZA-348). Previous studies in the area suggested that storm induced pup mortality may significantly influence the population dynamics of the Black Rocks seal colony (Shaughnessy, 1982). Therefore it was necessary to collect information on the intensity and frequency of storms during the pupping season (November/December). Subsequently, a temporary weather station was errected on Bird Island. Information on storms, and the general climatic conditions of the area, was collected daily from this station over a 3 year period.

This report describes the general climatic conditions of the Bird Islands for the 3 year period, from December 1992 to January 1996. Information on the impact of storms on seal pups is presented elsewhere (Stewardson, 1999).

MATERIALS AND METHODS

Study site

Bird Island is *c*. 9 m above sea level and measures *c*. 19 ha in area. Much of the island is covered by a thick growth of *Mesembryan themum*, *Tetragonia* and *Chenopodium* (Rand, 1963).

Stag Island (33^{o} 50.00’S, 26^{o} 17.00’E) lies *c*. 450 m NW of the northern coast of Bird Island, and measures 1 129 m^{2} in area. It has a raised central shingle beach which is sparely vegetated. Seal Island (33^{o} 50.00’S, 26^{o} 17.00’E) is larger in size (6 479 m^{2} in area) and lies *c*. 720 m NW of the NW corner of Bird Island. The two islands are joined by a reef which extends westward from Stag Island (Rand, 1963; Chart SAN 1025).

Black Rocks (33^{o} 50.25’S, 26^{o} 15.87’E) lies *c*. 1 080 m W-SW of Seal Island and consists of 5 small outcrops partially joined together by a reef of drying and submerged rocks. It is: situated 8–9 km off-shore (not sheltered by headlands); small in size (the largest rocky outcrop is 8 360 m^{2}); and low-lying (the largest outcrop is 6 m above mean sea level) (Rand, 1963, 1972; Chart SAN 1025). Therefore it is particularly susceptible to high seas. In 1992 the estimated seal population was 2 315 seals, and in 1996 it was 1 480 seals (Marine & Coastal Management, Unpubl. data).

The island complex is composed of quartzitic sandstones of the Table Mountain Group, of the Cape Supergroup. The sandstones are essentially Palaeozoic (Ordovician) (Sven Coles, pers. comm.; Bremner & Day, 1991).

Collection of data

On November 26, 1992 a temporary weather station was established on Bird Island. Information on air temperature, SST, rainfall, wind direction, wind speed and swell height, was collected daily from December 9, 1992 to January 31, 1996.

Maximum and minimum air temperatures (^{0}C) were read once daily at 0800 hrs from a standard mercury thermometer exposed in a Stevenson screen. Sea surface temperature (^{0}C) measurements

Fig. 1 Map of Algoa Bay, showing the Bird Islands including Black Rocks seal colony.

were read once daily at 0800 hrs from a standard mercury thermometer, and rainfall (mm) measurements were read once daily at 0800 hrs from a standard measuring cylinder.

Wind speed (knots) and direction were measured using a pressure plate anemometer. This instrument was erected on the centre of the island (on the northeast side of the path between the headman's house near the jetty and the helipad). Observations of wind activity were recorded thrice daily at 0800 hrs, 1400 hrs and 1800 hrs. The anemometer was monitored for 1–2 minutes before each reading was taken.

Swell height was recorded thrice daily at 0800 hrs, 1400 hrs and 1800 hrs. 'Subjective estimates' were based on visual observation of the water surface within several meters of the island.

Statistical analysis

Statistical analysis and graphics were implemented in Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1). Smooth curves for air temperature and SST were produced using the S-PLUS function ksmooth which performs scatter-plot smoothing using kernel estimates (Venables & Ripley, 2000). The standard normal density was used for the smoothing kernel. The kernel bandwidth smoothing parameter *h* controlled the degree of smoothing applied to the data and was set at 30 days (1 month).

RESULTS

Air temperature

Daily air temperature[1] ranged from 9°C to 33°C. Minimum temperate was recorded in winter (June 29–30, 1994; July 18, 1995; August 6 & 22, 1993) and maximum temperature was recorded in summer (February 21, 1994).

Mean monthly maximum temperature increased slightly in November; peaked in January/February (26°C); and then declined slowly throughout autumn, reaching a low in winter and early/mid spring (21°C to 22°C) (Table 1).

Table 1 ***Mean monthly maximum and mean monthly minimum air temperature (˚C) recorded at 0800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)***[1]

			Minimum temp. (˚C)		**Maximum temp. (˚C)**	
Month	***n***	**NR**	**Mean ± SE**	**Range**	**Mean ± SE**	**Range**
Summer						
December	93	0	16.0 ± 0.2	12–19	23.8 ± 0.3	18–29
January	93	0	17.7 ± 0.2	14–22	25.8 ± 0.2	21–32
February	84	0	18.1 ± 0.2	14–21	26.0 ± 0.2	19–33
	270	**0**	**17.2 ± 0.1**	**12–22**	**25.2 ± 0.2**	**18–33**
Autumn						
March	92	1	17.2 ± 0.2	13–22	25.3 ± 0.3	20–31
April	88	2	15.3 ± 0.2	11–19	23.2 ± 0.3	18–31
May	93	0	14.7 ± 0.2	10–18	22.5 ± 0.3	14–30
	273	**3**	**15.7 ± 0.1**	**10–22**	**23.7 ± 0.2**	**14–31**
Winter						
June	90	0	13.4 ± 0.2	9–18	21.9 ± 0.3	13–30
July	93	0	12.5 ± 0.2	9–16	21.7 ± 0.3	14–32
August	93	0	12.8 ± 0.2	9–16.5	21.0 ± 0.3	14–29
	276	**0**	**12.9 ± 0.1**	**9–18**	**21.5 ± 0.2**	**13–32**
Spring						
September	90	0	13.9 ± 0.2	10–17	21.2 ± 0.2	15–27
October	93	0	14.0 ± 0.2	10–17	21.3 ± 0.2	17–26
November	90	0	16.0 ± 0.2	11–19	23.5 ± 0.2	18–28
	273	**0**	**14.6 ± 0.1**	**10–19**	**22.0 ± 0.1**	**15–28**
Total	**1092**	**3**	**15.1 ± 0.1**	**9–22**	**23.1 ± 0.1**	**13–33**
December 1992	23	0	18.5 ± 0.2	17–20	26.4 ± 0.3	23–28
January 1996	30	1	18.1 ± 0.3	14–20	26.4 ± 0.3	22–31

n, number of observations at 0800 hrs.

NR, number of observations for 0800 hrs not recorded for that month.

[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.

Table 2 ***Mean maximum and mean minimum air temperature (˚C) recorded at 0800 hrs daily at Bird Island according to season and year (January 1, 1993 to December 31, 1995, n = 1 095 days)***

			Minimum temp. (˚C)		**Maximum temp. (˚C)**	
Month	***n***	**NR**	**Mean ± SE**	**Range**	**Mean ± SE**	**Range**
Summer						
1993	90	0	18.5 ± 0.2	14–22	26.1 ± 0.2	19–33
1994	90	0	16.7 ± 0.2	13–20	24.6 ± 0.2	18–30
1995	90	0	16.5 ± 0.2	12–20	24.8 ± 0.3	18–31
	270	**0**	**17.2 ± 0.1**	**12–22**	**25.2 ± 0.2**	**18–33**
Autumn						
1993	89	3	16.7 ± 0.2	13–22	24.6 ± 0.3	18–31
1994	92	0	16.0 ± 0.2	10–19	23.9 ± 0.3	16–31
1995	92	0	14.6 ± 0.2	11–18.5	22.6 ± 0.3	14–30
	273	**3**	**15.7 ± 0.1**	**10–22**	**23.7 ± 0.2**	**14–31**
Winter						
1993	92	0	13.3 ± 0.2	9–18	22.1 ± 0.3	15–32
1994	92	0	13.0 ± 0.2	9–18	21.4 ± 0.4	13–30
1995	92	0	12.4 ± 0.2	9–16.5	21.0 ± 0.3	14–29
	276	**0**	**12.9 ± 0.1**	**9–18**	**21.5 ± 0.2**	**13–32**
Spring						
1993	91	0	14.5 ± 0.2	12–19	21.7 ± 0.2	15–26
1994	91	0	14.3 ± 0.2	10–19	21.9 ± 0.2	16–27
1995	91	0	15.0 ± 0.2	11–19	22.3 ± 0.2	17–28
	273	**0**	**14.6 ± 0.1**	**10–19**	**22.0 ± 0.1**	**15–28**
All seasons						
1993	362	3	15.7 ± 0.1	9–22	23.6 ± 0.2	15–33
1994	365	0	15.0 ± 0.1	9–20	23.0 ± 0.2	13–31
1995	365	0	14.6 ± 0.1	9–20	22.6 ± 0.2	14–31
Total	**1092**	**3**	**15.1 ± 0.1**	**9–22**	**23.1 ± 0.1**	**13–33**

n, number of observations at 0800 hrs.

NR, number of observations for 0800 hrs not recorded for that year.

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[1] The air temperature data set was based on 1 092 days of records, i.e., data was not recorded during 3 days of the study

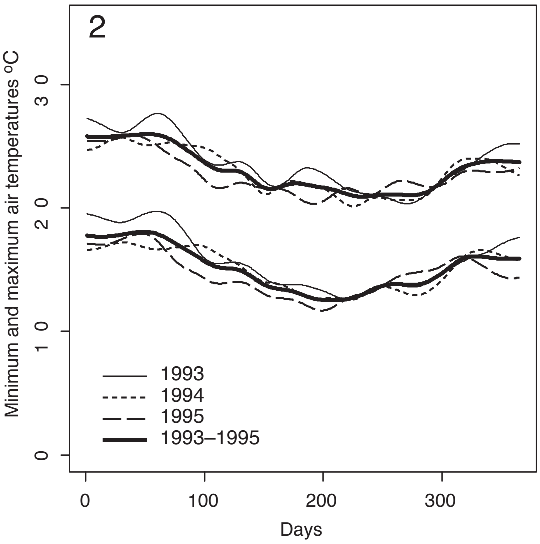

Fig. 2 Daily maximum and minimum air temperature (˚C) recorded at 0800 hrs at Bird Island (January 1, 1993 to December 31, 1995, *n* = 1 095 days).

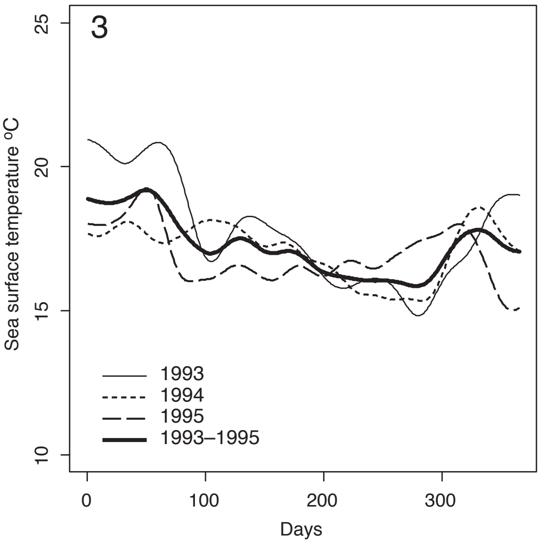

Fig. 3 Daily sea surface temperature (˚C) recorded at 0800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, *n* = 1 095 days).

Mean monthly minimum temperature increased slightly in September/October (14ºC) and November (16ºC); peaked in January/February (18ºC); and then declined slowly throughout autumn, reaching a low in winter (12ºC to 13ºC) (Table 1).

Overall, mean annual air temperatures were slightly higher in 1993 and lowest in 1995. However, in spring, mean temperature recorded in 1995 exceeded mean temperatures recorded 1993 and 1994 (Table 2; Fig. 2).

Sea surface temperature

Sea surface temperatures[2] ranged from 12ºC to 23ºC. Minimum SST was recorded in summer (December 19 & 26, 1995). Maximum SST was recorded in autumn (March 7, 1993) and summer (January 3, 1993).

Mean monthly SST increased in November; peaked in January/February (19ºC); and then declined slowly throughout autumn, reaching a low in July–October (16ºC) (Table 3).

Overall, mean annual SST was slightly higher in 1993. However, in spring, mean SST recorded in 1995 exceeded mean temperatures recorded in 1993 and 1994 (Table 4; Fig. 3).

During summer, mean monthly SST was 17ºC to 19ºC; however, on two occasions, SST fell by 5ºC due to wind induced upwelling:

(i) On December 12, 1995, strong easterly winds (up to 25 knots) were recorded, resulting in SST to fall to 13ºC on December 13–14. By December 17, SST gradually increased to 14ºC. Strong easterly winds (up to 20 knots) blew in the afternoon/evening causing SST to drop to 12.5ºC on December 18, and to 12ºC on December 19.

(ii) On December 24, 1995, strong easterly winds (up to 28 knots) were recorded, resulting in SST to fall from 17ºC to 12.5ºC on December 25, and to 12ºC on December 26.

Table 3 ***Mean monthly sea surface temperature (˚C) recorded at 0800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)***[1]

Month	*n*	NR	SST (˚C) Mean ± SE	Range
Summer				
December	93	0	17.4 ± 0.2	12–22
January	93	0	18.8 ± 0.2	15–23
February	84	0	19.2 ± 0.2	15.5–22
	270	**0**	**18.4 ± 0.1**	**12–23**
Autumn				
March	92	1	18.1 ± 0.2	14–22.5
April	90	0	17.0 ± 0.1	13.5–19.5
May	93	0	17.4 ± 0.1	15–19
	275	**1**	**17.5 ± 0.1**	**13.5–22.5**
Winter				
June	82	8	17.1 ± 0.1	15–19
July	92	1	16.4 ± 0.1	14.5–18
August	93	0	16.1 ± 0.1	14–18
	267	**9**	**16.5 ± 0.1**	**14–19**
Spring				
September	90	0	16.0 ± 0.1	14–18
October	93	0	16.0 ± 0.2	13–19.5
November	89	1	17.7 ± 0.1	14.5–20
	272	**1**	**16.6 ± 0.1**	**13–20**
Total	**1084**	**11**	**17.3 ± 0.1**	**12–23**
December 1992	22	1	20.7 ± 0.2	19–22
January 1996	30	1	19.4 ± 0.4	14–22

n, number of observations at 0800 hrs.
NR, number of observations for 0800 hrs not recorded for that month.
[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.

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[2] The SST data set was based on 1 084 days of records, i.e., data was not recorded during 11 days of the study.

Table 4 *Mean sea surface temperature (˚C) recorded at 0800 hrs daily at Bird Island according to season and year (January 1, 1993 to December 31, 1995, n = 1 095 days)*

Month	*n*	NR	SST (˚C) Mean ± SE	Range
Summer				
1993	90	0	20.0 ± 0.1	15.5–23
1994	90	0	17.8 ± 0.1	15–20
1995	90	0	17.5 ± 0.2	12–21
	270	**0**	**18.4 ± 0.1**	**12–23**
Autumn				
1993	92	0	18.4 ± 0.2	14.5–22.5
1994	92	0	17.7 ± 0.1	15–19.5
1995	91	1	16.4 ± 0.1	13.5–20.5
	275	**1**	**17.5 ± 0.1**	**13.5–22.5**
Winter				
1993	85	7	16.5 ± 0.1	15–18.5
1994	92	0	16.6 ± 0.1	14–19
1995	90	2	16.4 ± 0.1	14.5–18
	267	**9**	**16.5 ± 0.1**	**14–19**
Spring				
1993	91	0	15.9 ± 0.1	13–19
1994	90	1	16.4 ± 0.2	13–20
1995	91	0	17.4 ± 0.1	15–20
	272	**1**	**16.6 ± 0.1**	**13–20**
All seasons				
1993	358	7	17.7 ± 0.1	13–23
1994	364	1	17.1 ± 0.1	13–20
1995	362	3	16.9 ± 0.1	12–21
Total	**1084**	**11**	**17.3 ± 0.1**	**12–23**

n, number of observations at 0800 hrs.
NR, number of observations for 0800 hrs not recorded for that year.

Rainfall

Daily rainfall[3] ranged from 0–98 mm. Maximum rainfall was recorded on December 28, 1994 (65 mm), January 14, 1995 (98 mm) and September 22, 1993 (83 mm).

Mean monthly rainfall was very low (0.9 mm) in July and October, and peaked (2.2–3.0 mm) in December, January and September (Table 5).

Mean annual rainfall was 1.7 mm in 1993 and 1995, and slightly lower (1.6 mm) in 1994 (Table 6). Although mean monthly rainfall varied considerably between years, total annual rainfall was *c.* 600 mm (Table 7).

Wind direction

When all wind direction[4] data were combined, irrespective of time of day or season, it was apparent that wind direction had a westerly dominance, with a shift towards the easterly-component winds in summer (Fig. 4–7; Appendix 1–3).

Northerly-component winds (N, N-NE, N-NW)

N-NW winds were the most dominant of the northerly-component winds. N-NW winds generally developed in the mornings (land breeze) and were most frequent in winter.

Table 5 *Mean monthly rainfall (mm) recorded at 0800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)*[1]

Month	*n*	NR	Rainfall (mm) Mean ± SE	Range
Summer				
December	93	0	3.0 ± 0.9	0.0–65.0
January	92	1	2.3 ± 1.1	0.0–98.4
February	84	0	1.2 ± 0.4	0.3–0.8
	269	**1**	**2.2 ± 0.5**	**0.0–98.4**
Autumn				
March	93	0	1.2 ± 0.5	0.0–31.7
April	90	0	1.6 ± 0.4	0.0–18.4
May	92	1	1.2 ± 0.3	0.0–22.9
	275	**1**	**1.3 ± 0.2**	**0.0–31.7**
Winter				
June	90	0	1.8 ± 0.7	0.0–48.5
July	93	0	0.9 ± 0.4	0.0–20.6
August	93	0	1.5 ± 0.4	0.0–23.2
	276	**0**	**1.4 ± 0.3**	**0.0–48.5**
Spring				
September	90	0	2.5 ± 1.0	0.0–83.0
October	93	0	0.9 ± 0.3	0.0–16.5
November	90	0	1.6 ± 0.6	0.0–41.0
	273	**0**	**1.7 ± 0.4**	**0.0–83.0**
Total	**1093**	**2**	**1.6 ± 0.2**	**0.0–98.4**
December 1992	23	0	0.3 ± 0.3	0.0–6.1
January 1996	30	1	1.1 ± 0.4	0.0–9.0

n, number of observations at 0800 hrs.
NR, number of observations for 0800 hrs not recorded for that month.
[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.

Table 6 *Mean annual rainfall (mm) recorded at 0800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)*

Year	*n*	NR	Rain (days)	No rain (days)	Rainfall mean ± SE (mm)	Range (mm)	Total
1993	365	0	87 (24%)	278 (76%)	1.7 ± 0.4	0–83.0	621.3
1994	365	0	101 (28%)	264 (72%)	1.6 ± 0.3	0–65.0	587.3
1995	363	2	109 (30%)	254 (70%)	1.7 ± 0.3	0–98.4	573.7

n, number of observations at 0800 hrs.
NR, number of observations for 0800 hrs not recorded for that month.

[3] The SST data set was based on 1 093 days of records, i.e., data was not recorded during 2 days of the study.
[4] Wind speed/direction data set was based on 3 272 recording periods, i.e., data was not recorded during 13 recording periods. Zero wind speed was recorded on 49 recording periods.

Table 7 ***Total monthly rainfall (mm) recorded at 0800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)[1]***

			Total rainfall (mm)			
Month	***n***	**NR**	**1993**	**1994**	**1995**	**1993–1995**
Summer						
December	93	0	86.6	157.5	32.7	**276.8**
January	92	1	52.8	39.3	115.5	**207.2**
February	84	0	22.1	40.3	35.8	**98.2**
	269	**1**	**161.5**	**237.1**	**184.0**	**582.6**
Autumn						
March	93	0	7.2	46.2	60.3	**113.7**
April	90	0	41.6	23.1	76.6	**141.3**
May	92	1	16.0	37.0	55.4	**108.4**
	275	**1**	**64.8**	**106.3**	**192.3**	**363.4**
Winter						
June	90	0	129.6	21.5	6.4	**157.5**
July	93	0	8.0	48.5	30.9	**87.4**
August	93	0	56.1	69.4	13.0	**138.5**
	276	**0**	**193.7**	**139.4**	**50.3**	**383.4**
Spring						
September	90	0	148.9	33.5	40.9	**223.3**
October	93	0	11.6	48.3	24.3	**84.2**
November	90	0	40.8	22.7	81.9	**145.4**
	273	**0**	**201.3**	**104.5**	**147.1**	**452.9**
Total	**1093**	**2**	**621.3**	**587.3**	**573.7**	**1782.3**
December 1992	23	0	–	–	–	6.5
January 1996	30	1	–	–	–	31.8

n, number of observations at 0800 hrs.
NR, number of observations for 0800 hrs not recorded for that month.
[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.

Southerly-component winds (S, S-SE, S-SW)

S-SW winds were the most dominant of the southerly-component winds. S-SW winds generally developed in the afternoons (sea breeze) and were most frequent in spring and summer.

Easterly-component wind (E, E-SE, E-NE)

E-NE winds were the most dominant of the easterly-component winds. E-NE winds were frequent throughout the year; E winds were frequent in spring, summer and autumn; while E-SE winds were frequent in spring and summer. E winds were more dominant than E-NE winds in summer.

Westerly-component winds (W, W-NW, W-SW)

W-SW winds were the most dominant westerly-component winds. W-SW and W-NW winds were frequent throughout the year, especially in winter; while W winds were most frequent in autumn. W-NW winds generally blew in the mornings, whereas W-SW winds tended to blow throughout the day. This was enhanced and by the land/sea breeze effect.

Other wind directions (NW, NE, SE, SW)

SW winds were frequent throughout the year, especially in summer, autumn and spring. NW winds were frequent in winter (mornings).

Wind speed

Spring was the windiest season. Wind speed of 0–5 knots (calm to slight breeze) were most frequent in autumn and least frequent in spring (Fig. 4–7).

Wind speeds[4] ≥ 28 knots (near gale or greater) were recorded in all seasons (Table 8). Gales were most frequent in May–August and October. Gales were predominantly westerly (W-SW) in autumn and winter; and easterly (E-ENE) and westerly (W-SW) in spring.

Median wind speed was consistently stronger in the afternoons (*c.* 14.0 knots)/evenings (*c.* 13.0 knots) than in the mornings (*c.* 11.0 knots). In the mornings, median monthly wind speed was highest in June (15.0 knots); in the afternoons, median speed was highest in June (15.5 knots) and October (15.0 knots); and in the evenings, median speed was highest in November (16.0 knots) (Appendix 1–3).

Table 8 ***Gale force winds (days) recorded at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)***

		Number of days with gales			
Wind direction	**Component winds**	**Summer**	**Autumn**	**Winter**	**Spring**
N	N	0	0	0	0
	N-NE	0	0	0	0
	N-NW	0	0	0	0
	NW	0	0	2	0
	NE	0	1	0	0
E	E	0	1	0	5
	E-SE	1	0	0	1
	E-NE	2	0	1	5
	SE	0	0	0	0
S	S	0	0	0	0
	S-SW	0	0	0	0
	S-SE	1	0	0	0
	SW	2	1	1	2
W	W	1	2	3	1
	W-NW	0	0	4	0
	W-SW	2	14	15	6
Total		**9[1] (0)**	**19[2] (3)**	**26[3] (7)**	**20[4] (3)**

(), number of consecutive days (2/3 days) with gale force winds.
Wind data for December 9–31, 1992 and January 1–31, 1996 was excluded from analysis.
During the 3 year study: [1]gales occurred on 6 days in December; [2]gales occurred on 16 days in May; [3]gales were distributed equally winter; [4]gales occurred on 15 days in October.

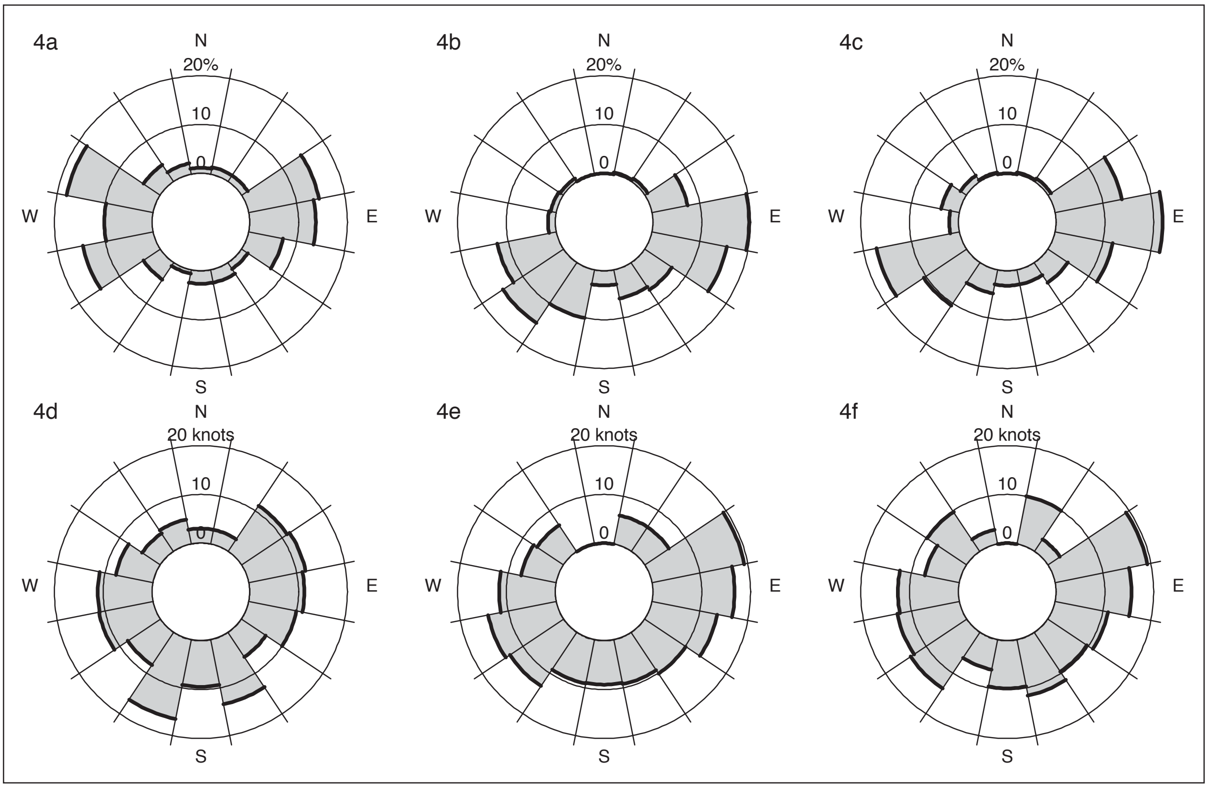

Fig. 4 Wind-rose diagrams for Bird Island for summer showing wind frequency (%) in various directions* at: (a) 0800 hrs, (b) 1400 hrs and (c) 1800 hrs; and mean wind speed (knots) in various directions at: (d) 0800 hrs, (e) 1400 hrs and (f) 1800 hrs (January 1, 1993 to December 31, 1995, *n* = 1 095 days).

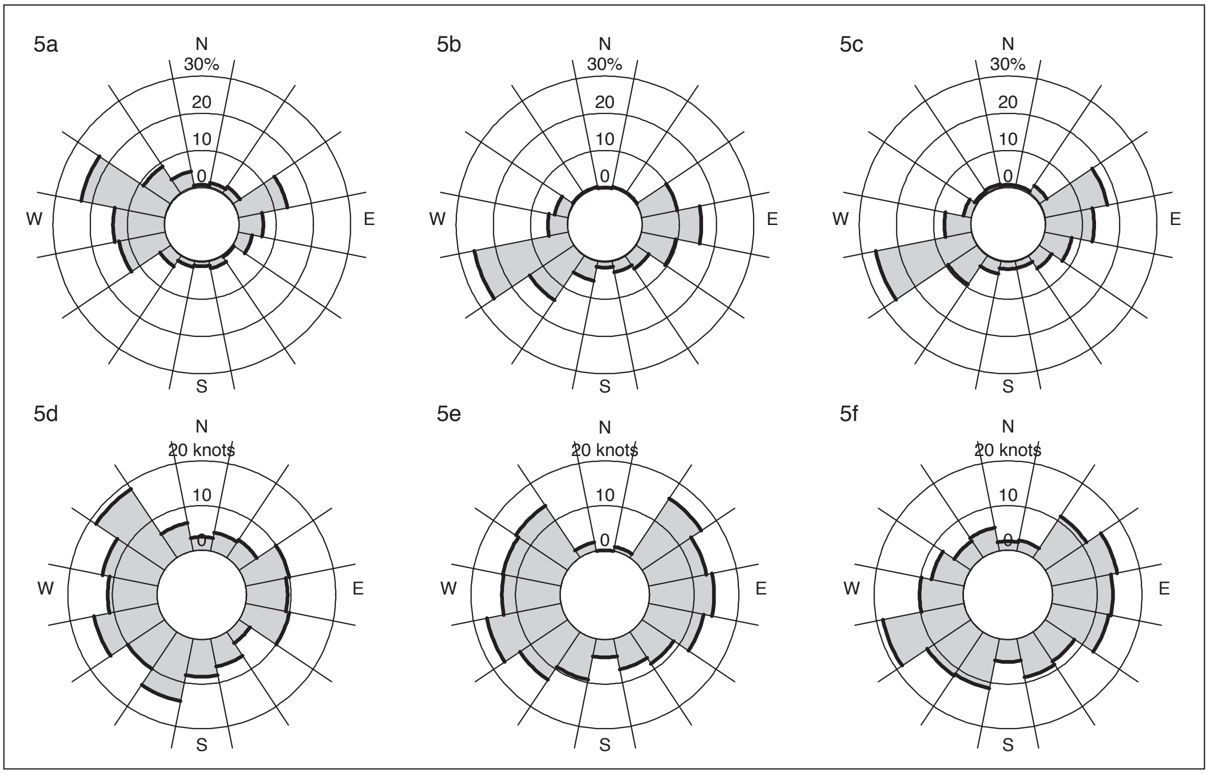

Fig. 5 Wind-rose diagrams for Bird Island for autumn showing wind frequency (%) in various directions at: (a) 0800 hrs, (b) 1400 hrs and (c) 1800 hrs; and mean wind speed (knots) in various directions at: (d) 0800 hrs, (e) 1400 hrs and (f) 1800 hrs (January 1, 1993 to December 31, 1995, *n* = 1 095 days).

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* Wind direction was classified as follows: N (360°), NNE (22.5°), NE (45.0°), ENE (67.5°), E (90.0°), ESE (112.5°), SE (135.0°), SSE (157.5°), S (180.0°), SSW (202.5°), SW (225.0°), WSW (247.5°), W (270.0°), WNW (292.5°), NW (315.0°) or NNW (337.5°).

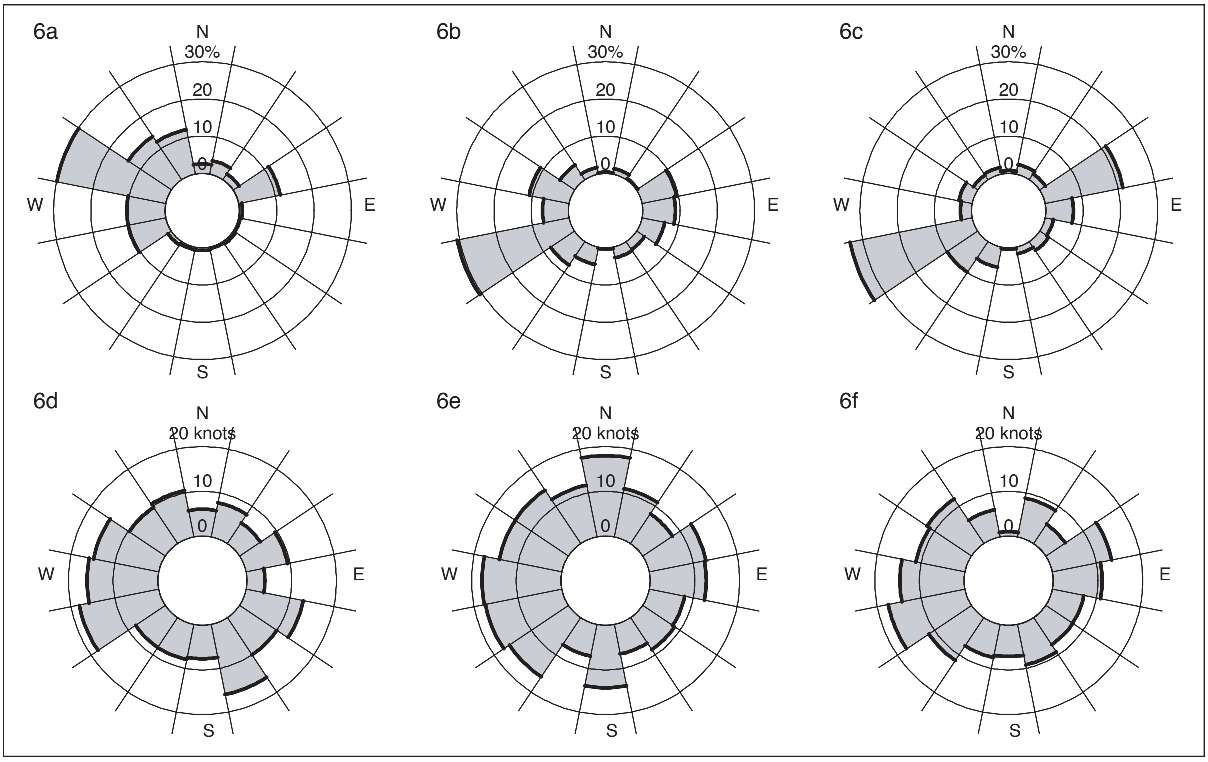

Fig. 6 Wind-rose diagrams for Bird Island for winter showing wind frequency (%) in various directions at: (a) 0800 hrs, (b) 1400 hrs and (c) 1800 hrs; and mean wind speed (knots) in various directions at: (d) 0800 hrs, (e) 1400 hrs and (f) 1800 hrs (January 1, 1993 to December 31, 1995, *n* = 1 095 days).

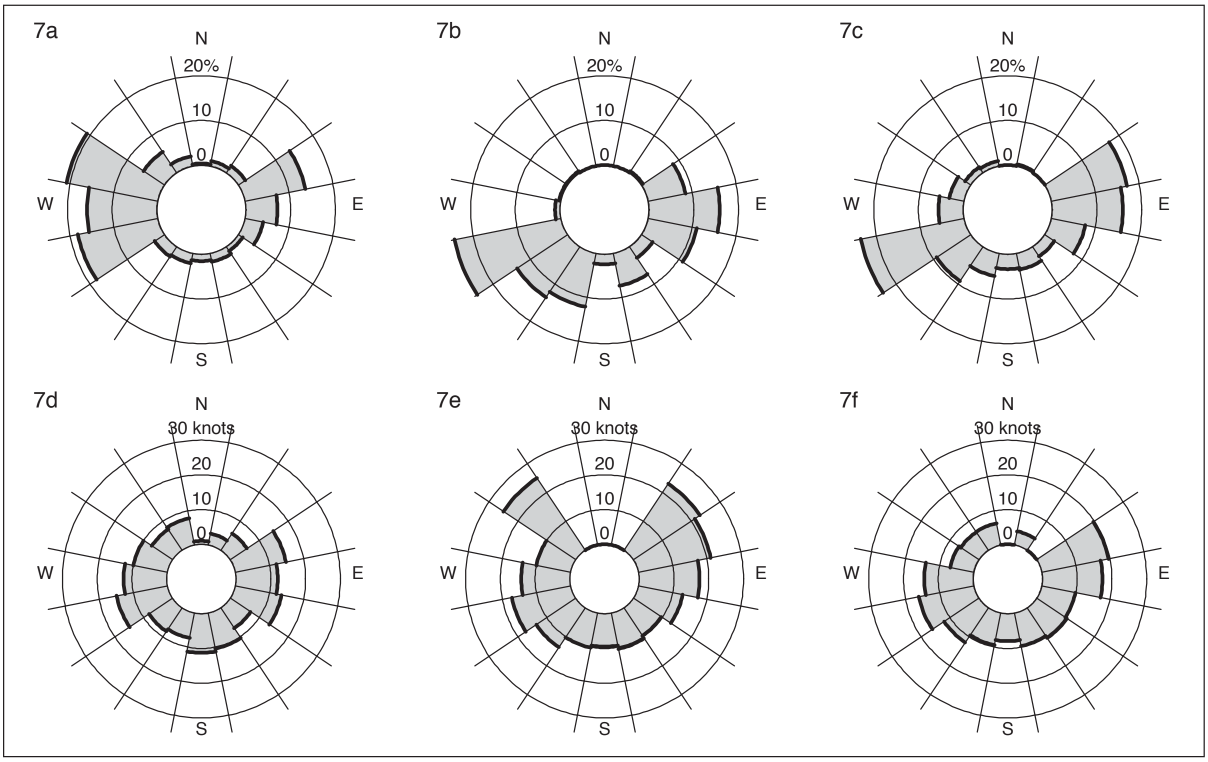

Fig. 7 Wind-rose diagrams for Bird Island for spring showing wind frequency (%) in various directions at: (a) 0800 hrs, (b) 1400 hrs and (c) 1800 hrs; and mean wind speed (knots) in various directions at: (d) 0800 hrs, (e) 1400 hrs and (f) 1800 hrs (January 1, 1993 to December 31, 1995, *n* = 1 095 days).

Swell height

'Estimated' swell height[5] ranged from 0.5–6.0 m (Table 9). Large swells (5–6 m) were recorded in March (4 days), April (3 days), July (2 days), September (2 days), October (6 days) and December (2 day).

Table 9 ***Estimated mean monthly swell height recorded thrice daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)[1]***

		Swell height (m)		
Month	***n***	**NR**	**Mean ± SE**	**Range**
Summer				
December	277	2	1.6 ± 0.05	0.5–5.0
January	277	2	1.2 ± 0.04	0.5–4.0
February	250	2	1.5 ± 0.05	0.5–4.0
	804	**6**	**1.4 ± 0.03**	**0.5–5.0**
Autumn				
March	279	0	1.8 ± 0.08	0.5–5.0
April	269	1	1.7 ± 0.07	0.5–5.0
May	278	1	1.4 ± 0.04	0.5–4.0
	826	**2**	**1.7 ± 0.04**	**0.5–5.0**
Winter				
June	269	1	1.7 ± 0.05	0.5–4.0
July	278	1	1.7 ± 0.05	0.5–5.0
August	277	2	1.5 ± 0.04	0.5–4.0
	824	**4**	**1.6 ± 0.03**	**0.5–5.0**
Spring				
September	270	0	1.7 ± 0.05	0.5–5.0
October	279	0	1.6 ± 0.07	0.5–6.0
November	268	2	1.3 ± 0.05	0.5–4.0
	817	**2**	**1.5 ± 0.03**	**0.5–6.0**
Total	**3271**	**14**	**1.6 ± 0.02**	**0.5–6.0**
December 1992	67	2	1.0 ± 0.05	0.5–2.0
January 1996	92	1	2.3 ± 0.09	1.0–4.5

n, number of observations at 0800 hrs, 1400 hrs and 1800 hrs.
NR, number of observations for 0800 hrs, 1400 hrs and 1800 hrs not recorded for that month.
[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.

DISCUSSION

Air temperature

At the Bird Islands, daily air temperature ranged from 9°C to 33°C, with mean monthly temperatures peaking in summer and reaching a low in winter and early/mid spring (present study). Daily change in air temperature is primarily attributed to radiation changes, with temperatures generally rising between dawn and midafternoon. Nocturnal cooling continues until about dawn.

Previous studies within Algoa Bay indicate that incoming solar radiation varies from *c.* 350 Wm^{-2} in summer to *c.* 140 Wm^{-2} in winter (Goschen, 1991). Therefore, at the Birds Islands, mean maximum and mean minimum air temperatures may differ by 4°C or 5°C in mid-summer and in mid-winter (present study).

Sea surface temperature

Sea surface temperature within Algoa Bay decreases from the shoreline to the shelf, and then increase again to the Agulhas Current (Goschen, 1991). A strong thermocline (surface layer 15–20°C; bottom layer 9–12°C) is present over the continental shelf off Algoa Bay (Goschen, 1991). However, the shallow inshore waters are generally well mixed due to wind-forcing (Goschen & Schumann, 1988).

At the Bird Islands, daily SST ranged from 12°C to 23°C and varied seasonally, with mean monthly temperatures remaining low from July to October, and peaking in January/February (present study). Seasonal variability in the surface heat fluxes, and mass transports of water, are the primary factors influencing temperature structure within Algoa Bay (Goschen, 1991).

Minimum SST's within Algoa Bay are usually caused by one of the following. Firstly, localised easterly winds can cause upwelling at Cape Recife and Cape Padrone, resulting in advection of the cold bottom water into adjacent areas (Schumann, Perrins & Hunter, 1982; Goschen, 1991; present study). Secondly, upwelling associated with the inshore boundary of the Agulhas Current (*c.* 44 km off Cape Padrone and *c.* 60 km off Cape Recife) can introduce cold water (12°C or 13°C) into Algoa Bay (Walker, 1986; Schumann, 1987; Goschen, 1988; Dr Ian Hunter, pers. comm.). Thirdly, upwelling forced by the Agulhas Current can introduce cold water onto the shelf which may occasionally penetrate Algoa Bay (Eagle & Orren, 1985; Schumann, 1987; Swart & Largier, 1987; Goschen & Schumann, 1988; Schumann, Ross & Goschen, 1988).

Maximum SST's within Algoa Bay are generally associated with the Agulhas Current. The core of this current (max. temp 26°C) generally flows just beyond the shelf break, i.e., 70 km off shore for Algoa Bay (Pearce, 1977; Gründlingh, 1983). The Agulhas Current separates from the shelf break west of Algoa Bay. Downstream of this region, meanders and frontal eddies of the Agulhas Current increase in dimension (Goschen, 1991). Plumes of warmer water attached to eddies may cross the shelf edge over the continental shelf, advecting warmer water across the Agulhas Bank, causing SST to rise to 24°C^{+}, from Cape Agulhas to Algoa Bay (Eagle & Orren, 1985; Swart & Largier, 1987; Goschen & Schumann, 1988; Lutjeharms, 1981; Dr Ian Hunter, pers. comm.). East London does not benefit from these large episodic core meanders, i.e., maximum SST's are in the low 20's.

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[5] Swell height data set was based on 3 273 recording periods, i.e., data was not recorded during 12 recording periods.

Rainfall

The southwestern Cape has winter rainfall, while the east coast has a summer rainfall. The Eastern Cape coast lies in an intermediate situation (Schultze, 1965). At the Bird Islands, rain falls through out the year with highest rainfall in summer (present study). Total annual rainfall (*c*. 600 mm) is similar to the mainland (e.g., *c*. 624 mm at Port Elizabeth; Garth Sampson, pers. comm.).

Wind speed and direction

At the Bird Islands, the prevailing winds (W-SW and E-NE) are parallel with the general orientation of the coast (Illenberger 1986; Goschen, 1988, 1991; Schumann & Martin, 1991; present study). Westerly-component winds are common for most of the year, with easterly-component winds dominate in summer (Schumann, 1992; present study). The seasonal dominance of easterly- and westerly-component winds at the Bird Islands is caused by the semipermanent South Atlantic and South Indian anticyclones which form part of the belt of anticyclonic centers occurring within the average limits of *c*. 27^0–38^0S. This belt moves seasonally by 4–6^0 (latitude) causing the South Atlantic anticyclone to ridge eastward over the southern tip of Africa in winter and lie further south in summer (Schumann, 1992).

Land/sea breezes form an important component of local winds at the Bird Islands (Roberts, 1990; Goschen, 1991; present study). At these islands the sea breeze (S-SW) is most frequent in spring and summer, and the land breeze (N-NW) is most frequent in winter (present study). Considering that variation in air temperature is large if the wind is off the land, and small if wind is off the sea, diurnal air temperatures at these islands are more variable in winter (9^0C to 32^0C) than in spring (10^0C to 28^0C) and summer (12^0C to 33^0C) (present study).

Water movement in the nearshore region of Algoa Bay is mainly due to wind forcing (Roberts, 1990). In summer, easterly component winds increase in strength and frequency causing localised upwelling at the major Capes and a subsequent fall is SST (Schumann, Ross & Goschen, 1988; Goschen, 1991). Localised upwelling enhances primary productivity by bringing nutrients into the euphotic zone, promoting the growth of plankton which indirectly benefits large predators by increasing prey availability. In the present study, SST fell to 12^0C in summer in association with strong easterly winds. No case of upwelling was observed in the absence of easterly-component winds in the summer months (present study). In winter, the frequency of easterly-component winds decreases (Goschen, 1991; present study), and the depth of the surface isothermal layer over the shelf increases, resulting in a reduction in wind driven upwelling (Goschen, 1991).

Swell height

The most common swell along the Eastern Cape coast is from the SW, usually originating from low pressure systems moving from west to east, over the southern ocean (Dr Ian Hunter, pers. comm.).

Strong, persistent south westerly winds, with a fetch of ≥ 1200 nautical miles in the Southern Ocean, generate a fully developed sea with waves reaching maximum height and length by the time they reach Algoa Bay (Bremner, 1991). Abnormal waves in excess of 18 m have been reported in the vicinity of the shelf break. Occasionally waves ≥ 10 m enter Algoa Bay (Bremner, 1991). In the present study abnormally large waves were not recorded. Maximum wave height was 6 m.

CONCLUSION

Overall, climate at the Bird Islands is not severe, with moderate air temperatures ranging from 9^0C to 33^0C; SST's ranging from 12^0C to 23^0C; a total annual rainfall of c. 600 mm; and relatively strong winds predominantly W-SW and E-NE.

In order to fully understand the complex interactions between climate and the resident seal population, continued monitoring of climatic conditions at the Bird Islands is required. Particular attention should be given to: (i) pup mortality relative to storms; (ii) the timing of the pupping season relative to upwelling events; and (iii) the effects of climate on prey species relative to the distribution/abundance patterns of seals throughout their breeding range.

Considering that Black Rocks is often surrounded by heavy breakers, ongoing behavioural studies examining the impact of high temperatures on: (i) daily activities of seals, (ii) pup survival, and (iii) duration of territorial tenure, would not be feasible.

Climate data collected at the offshore Bird Islands (present study) should be compared with climate data collected from the mainland (at Port Elizabeth Airport). Similarities and differences between the two sites can then be quantified, increasing our overall understanding of the climate in this region.

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Appendix 1 ***Mean monthly wind speed recorded at 0800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)[1]***

			Wind speed (knots)		
Month	***n***	**NR**	**Mean ± SE**	**Median**	**Range**
Summer					
December	93	0	10.4 ± 0.6	11.0	1–20
January	93	0	9.6 ± 0.7	10.0	0–30+
February	84	0	8.9 ± 0.6	8.0	0–20
	270	**0**	**9.7 ± 0.4**	**10.0**	**0–30+**
Autumn					
March	92	1	8.5 ± 0.5	8.0	0–24
April	90	0	10.2 ± 0.7	10.0	0–30+
May	93	0	11.7 ± 0.8	12.0	0–30+
	275	**1**	**10.1 ± 0.4**	**10.0**	**0–30+**
Winter					
June	90	0	14.4 ± 0.8	15.0	1–30+
July	92	1	12.0 ± 0.7	11.0	0–30+
August	93	0	10.8 ± 0.7	10.0	0–30+
	275	**1**	**12.4 ± 0.4**	**12.0**	**0–30+**
Spring					
September	90	0	11.3 ± 0.8	10.0	0–30+
October	93	0	11.6 ± 0.6	11.0	0–30+
November	90	0	11.7 ± 0.7	12.0	1–30+
	273	**0**	**11.5 ± 0.4**	**11.0**	**0–30+**
Total	**1093**	**2**	**10.9 ± 0.2**	**11.0**	**0–30+**
December 1992	22	1	11.2 ± 0.9	10.0	4–20
January 1996	31	0	8.1 ± 0.7	9.0	3–17

n, number of observations at 0800 hrs.

NR, number of observations for 0800 hrs not recorded for that month.

[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.

Appendix 2 ***Mean monthly wind speed recorded at 1400 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)[1]***

			Wind speed (knots)		
Month	***n***	**NR**	**Mean ± SE**	**Median**	**Range**
Summer					
December	93	0	13.7 ± 0.6	13.0	2–30$^+$
January	93	0	12.5 ± 0.6	12.0	1–30$^+$
February	84	0	13.7 ± 0.7	14.0	0–28
	270	**0**	**13.3 ± 0.4**	**13.0**	**0–30+**
Autumn					
March	90	3	12.2 ± 0.7	11.5	0–30$^+$
April	88	2	13.9 ± 0.7	14.5	0–30$^+$
May	93	0	13.2 ± 0.9	13.0	0–30$^+$
	271	**5**	**13.1 ± 0.4**	**13.0**	**0–30+**
Winter					
June	90	0	15.0 ± 0.7	15.5	2–30$^+$
July	93	0	14.0 ± 0.7	14.0	2–30$^+$
August	91	2	13.5 ± 0.8	12.0	2–30$^+$
	274	**2**	**14.1 ± 0.4**	**14.0**	**2–30+**
Spring					
September	90	0	14.5 ± 0.8	13.0	4–30$^+$
October	93	0	15.4 ± 0.7	15.0	3–30$^+$
November	89	1	14.7 ± 0.7	14.0	2–30$^+$
	272	**1**	**14.9 ± 0.4**	**14.0**	**2–30+**
Total	**1087**	**8**	**13.8 ± 0.2**	**14.0**	**0–30+**
December 1992	23	0	13.8 ± 0.9	14.0	6–22
January 1996	30	1	12.0 ± 1.0	11.0	3–25

n, number of observations at 1400 hrs.

NR, number of observations for 1400 hrs not recorded for that month.

[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.

Appendix 3 ***Mean monthly wind speed recorded at 1800 hrs daily at Bird Island (January 1, 1993 to December 31, 1995, n = 1 095 days)[1]***

			Wind speed (knots)		
Month	***n***	**NR**	**Mean ± SE**	**Median**	**Range**
Summer					
December	93	0	13.4 ± 0.7	13.0	1–30+
January	93	0	12.7 ± 0.7	12.0	0–30+
February	83	1	13.0 ± 0.8	12.0	0–30+
	269	**1**	**13.1 ± 0.4**	**12.0**	**0–30+**
Autumn					
March	92	1	12.2 ± 0.7	12.5	0–30+
April	90	0	13.9 ± 0.8	14.0	0–30+
May	93	0	13.5 ± 0.9	12.0	0–30+
	275	**1**	**13.2 ± 0.5**	**13.0**	**0–30+**
Winter					
June	89	1	13.5 ± 0.8	14.0	0–30+
July	93	0	13.4 ± 0.8	12.0	1–30+
August	93	0	12.1 ± 0.8	10.0	1–30+
	275	**1**	**13.0 ± 0.5**	**12.0**	**0–30+**
Spring					
September	90	0	13.8 ± 0.7	14.0	1–30+
October	93	0	14.9 ± 0.8	14.0	0–30+
November	90	0	14.2 ± 0.8	16.0	2–30+
	273	**0**	**14.3 ± 0.4**	**14.0**	**0–30+**
Total	**1092**	**3**	**13.4 ± 0.2**	**13.0**	**0–30+**
December 1992	22	1	12.5 ± 1.1	11.0	6–25
January 1996	31	0	13.0 ± 1.0	11.0	4–25

n, number of observations at 1800 hrs.

NR, number of observations for 1800 hrs not recorded for that month.

[1] Data for December 9–31, 1992 and January 1–31, 1996 is presented separately at the end of this table.