Maternal and pup growth strategies of sympatric Antarctic and subantarctic fur seals at Ile de la Possession, Iles Crozet, Southern Indian Ocean

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Maternal and pup growth strategies of sympatric Antarctic and subantarctic fur seals at Ile de la Possession, Iles Crozet, Southern Indian Ocean

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Abstract

Otariid pinnipeds exhibit large variation in lactation duration, and pups wean at different times of cycles in marine productivity. Interspecific comparisons to understand the mechanisms driving variation in maternal care strategies and pup development are difficult due to inability to control for confounding effects of differences in environment. I investigated interspecific differences in foraging ecology, allocation of maternal resources into pups, and use of maternal resources by pups as they approach weaning, between sympatric Antarctic and subantarctic fur seals at Ile de la Possession, Iles Crozet, Southern Indian Ocean. Females of both fur seal species fed on the same myctophid fish prey over largely overlapping areas, with minor but important differences in the proportion of species consumed. SFS females showed less diel variation in diving behaviour, suggesting that they followed the nycthymeral migrations of their prey to a smaller extent than AFS. Diving occurred exclusively at night in both species, but SFS females dove deeper and for longer periods. AFS females had smaller aerobic dive limit (ADL), but had higher propensity to dive anaerobically. AFS females exploited more patches per unit time, and remained in them for briefer periods of time. AFS females foraged in patches of better quality, at the cost of greater foraging effort. Body shape differed significantly between species from birth, and growth involved the acquisition of a longer, more slender body with larger foreflippers in AFS. Allometric analysis showed that body shape differences present at birth were exacerbated during growth, so they were physically more mature at 100 d of age. Milk composition did not differ between species, and total energy intake was significantly higher in AFS at any given age. SFS pups had proportionally larger total body lipid reserves, and had lower resting and daily metabolic rates than AFS pups. Results suggest that, under comparable foraging conditions, maternal expenditure is larger in AFS, in response to a relatively briefer and more inflexible duration of lactation.

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The work presented here was, for me, the realization of a “dream” project for a doctoral thesis. This unique privilege was given to me by my co-supervisor Christophe Guinet at the Centre D’Etudes Biologiques de Chizé, France, who ensured the project received proper funding for gear and complex research logistics in a remote location. I am deeply grateful for the encouragement, discussions, and freedom to pursue my interests that he entrusted me with throughout these years. I will never forget the great times we shared in the field and in Chizé, where I have also learned a new language and made new friends.

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Co-authorship statement

I designed the research proposal for this thesis in agreement with my co-supervisors, Christophe Guinet (Centre D'Etudes Biologiques de Chizé) and Edward H. Miller (Memorial University). I am the principal author in all chapters and sections of this thesis, having performed all aspects of research from design, data collection in the field and laboratory, analyses, and manuscript preparation. My co-supervisors, Christophe Guinet and Edward H. Miller, co-authors and collaborators provided guidance and peer review during this process. Numerous other individuals provided help during field work and data analysis, and their contributions are described in the Acknowledgements section. The project was part of a larger programme funded by the Institut Polaire Français Paul Emile Victor (IPEV) for research in the French Antarctic and Subantarctic territories. All the material presented here is the result of my own work, except for Appendix B (led by Frédéric Bailleul) and Appendix C (led by Dr. John P. Y. Arnould), which were concurrent and complementary projects, derived from my initial research proposal. I contributed initial ideas, efforts in data collection, and comments during manuscript preparation for these projects that complement Parts I and II of the thesis, respectively.

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Acronyms

Behaviour

ADL Aerobic dive limit.

IPQ Index of patch quality.

LFT Long foraging trip.

OFT Overnight foraging trip.

Equipment

PTT Platform Transmitter Terminal.

TDR Time-depth recorder.

Oceanography

ACC Antarctic Circumpolar Current.

APF Antarctic Polar Front.

ARF Agulhas Return Front.

CF Crozet Front.

PFZ Polar Frontal Zone.

SAF Subantarctic Front.

SST Sea surface temperature.

STF Subtropical Front.

TFZ Transition Frontal Zone.

Study system

AFS Antarctic fur seal.

MAE La Mare aux Elephants.

SFS Subantarctic fur seal.

Chapter 1

Introduction

1.1 Maternal care and offspring growth strategies: insights from comparisons among sympatric species and populations

Ecological segregation results from competitive exclusion whereby two species having the same ecological niche, the concept of space occupied by a given species, which includes both the physical space, as well as the functional role of the species (Hutchinson 1957), cannot coexist indefinitely. Thus, sympatric species should either have different ecological function in their ecosystem, and/or have different reproductive strategies, so that species coexistence remains possible. Coexistence is inversely related to phylogenetic distance among primates (Houle 1997), so the mechanisms involved are most suitably studied among closely related species (MacArthur and Levins 1967, Abrams 1983). Finding appropriate research models can, thus, be challenging because closely related species are not often found in sympatry or syntopy. However, carefully chosen models of insect communities (Dietrich and Wehner 2003), terrestrial (Schoener et al. 1979, Fedigan and Rose 1995, Jones and Barmuta 2000, Belant et al. 2006) and aquatic mammals (Parra 2006), reptiles (Dodson 1975, Webb et al. 2003), and birds (Ballance et al. 1997, Hull 1999) have provided useful insights into this topic.

Lactation is the main form of parental care in mammals and the most energetically expensive activity for females (Pond 1977, Gittleman and Thompson 1988), so it is expected to play an important role in determining mechanisms of coexistence among species (Farley and Robbins 1995, Fedigan and Rose 1995). Parents should adjust their behaviour so as to maximize their fitness under different interspecific competitive interactions (Wiens 1977, Clutton-Brock 1991*a*). Therefore, not only can comparisons of maternal strategies of sympatrically breeding mammals help to elucidate mechanisms of coexistence, but can also provide insights into what determines life history variation without the confounding effects of environmental differences. Maternal strategy is herein referred to as the suite of maternal behaviours that affect maternal investment in current offspring, such as the temporal pattern of energy delivery, the duration of lactation, and a mother's foraging behaviour allowing her to invest in offspring (Lee et al. 1991, Clutton-Brock 1991*b*). Offspring are not passive receivers of maternal investment, but can control the allocation of maternal resources to physical, physiological, and behavioural development (Horning and Trillmich 1999). The latter is herein referred to as an offspring's growth strategy (Moulton 1923, Vargas and Anderson 1996).

1.2 Study system

Sea lions and fur seals (Carnivora: Otariidae), are well suited for comparative studies of foraging ecology and maternal care strategies because: i) the degree of sexual dimorphism, social structure, and natural history are relatively uniform across the family, ii) males have no role in parental care beyond copulation, iii) milk delivery to the pup and foraging are temporally separated, such that lactating females have to periodically return to land to suckle their young after foraging trips to sea, and iv) they display large variation in lactation duration (4 to 36 months), so pups are weaned at different times of the year and stages of development, depending on the species (Figure 1.1). Some of these features are shared with the smallest phocid pinnipeds (Carnivora: Phocidae), but lactation is significantly briefer and pups are weaned at about the same time of the year among phocids in general (Figure 1.2). Otariids may be regarded as central place foragers during lactation and environmental changes in the vicinity of the rookery, as well as inter- and intraspecific interactions, would be expected to affect their maternal care strategies (Stephens et al. 1986, Boyd 1998).

The otariid "maternal strategy" here refers to the set of behaviours whereby females acquire energy at sea and transfer it to their young for growth and development (Boness and Bowen 1996). These behaviours can be divided into: i) at-sea behaviours, such as use of space for diving and travelling (e.g. time and depth distribution of dives, and swimming to and from food patches), which are associated with foraging, ii) the attendance or temporal pattern of visits to land for suckling young and resting vs. feeding at sea, and duration of lactation, and iii) milk delivery while ashore (time spent suckling, amount and quality of milk delivered). The pups' growth strategy includes the pattern of physical growth, and physiological and behavioural development (Figure 1.1).

Fur seals are shallow divers (<30 m) (Gentry and Kooyman 1986*a*), and most of their foraging dives occur at night as they feed on vertically migrating fish, cephalopods, and crustaceans, which are found near the surface during that time (Croxall et al. 1985, Gentry and Kooyman 1986*a*). The proximate factors responsible for such pattern are the spatial distribution of prey, its behaviour, size and energy density (Boyd 1996, Costa and Williams 1999). Because these prey-related characteristics usually vary over time, the dive pattern employed by fur seals may change seasonally and interannually (Costa et al. 1989, Boyd et al. 1994, Mattlin et al. 1998, Georges et al. 2000*b*). Distance to foraging grounds from the suckling site, time spent resting while at sea, and distance between food patches, have a significant impact on the energy budget of lactating females (Costa et al. 1989). Therefore, the amount and quality of maternal care is influenced by these behavioural choices and environmental conditions.

The way in which lactating females allocate their time to foraging at sea and suckling ashore determines how long pups must fast and how much time they have available for milk ingestion. Therefore, lactating females should distribute their time so as to balance the net amount of energy they can gain while at sea, against the amount of time their pups can fast without negative effects on their growth and development (Oftedal et al. 1987, Bowen 1991). Intra- and interspecific variation in this component of the maternal strategy is particularly large (Trillmich 1990, Francis et al. 1998). During periods of low food availability, fur seals mothers stay at sea longer and transfer less milk to the pup than at other times (Trillmich et al. 1991*b*). However, this does not explain the large interspecific differences in maternal attendance patterns among fur seals. Comparative studies of maternal attendance patterns in sympatric[1] Antarctic (*Arctocephalus gazella* (Peters, 1875)) and subantarctic fur seals (*Arctocephalus tropicalis* (Gray, 1872)) at Macquarie and Marion islands (Bester and Bartlett 1990, Goldsworthy 1999), showed small, but important, differences between both species and sites. Subantarctic fur seal females breeding in Amsterdam Island have much longer foraging trips than at Macquarie (11-23 days at Amsterdam, 3.8 days at Macquarie), but there is a window of foraging trip durations, associated with maternal characteristics, that maximizes pup growth rate (Georges and Guinet 2000*b*). Similarly, foraging trip duration of both species at

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[1] The term "syntopic", which refers to the condition of local sympatry, would be more appropriate here, but I will use "sympatric" to avoid confusion in comparisons with previous studies at other sites.

Macquarie Island showed a bimodal distribution that is untypical of the core of each species' distribution. Local environmental factors should, therefore, be accounted for in comparisons of attendance patterns and maternal strategies.

Because milk composition and pup demand change throughout lactation, the amount of time lactating females spend ashore is not useful to estimate energy intake by the pups (Gentry et al. 1986, Oftedal et al. 1987). Milk fat content and milk production in Antarctic (Arnould and Boyd 1995*b*), Northern (*Callorhinus ursinus* (L., 1758)) (Costa et al. 1986), and Australian (*Arctocephalus pusillus doriferus* (Wood Jones, 1925)) (Arnould and Hindell 1999) fur seals rise throughout most of lactation, and at least in Antarctic fur seals, they decrease in the last few weeks. In contrast, milk protein remains relatively constant. In Antarctic and Northern fur seals, these parameters have been shown to vary with pup age and mass (Costa et al. 1986, Arnould et al. 1996*a*), as well as with changes in food availability (Arnould et al. 1996*a*). Furthermore, on the scale of foraging cycles, milk fat content and milk consumption vary with the duration of the preceding foraging trip in these and other species (Arnould et al. 1996*a*, Costa 1991, Ochoa-Acuña et al. 1999). Therefore, part of the variation in pup growth rates and weaning masses that are not accounted for by maternal attendance patterns, may be explained by differences in milk intake and composition.

Pinnipeds are among the most sexually dimorphic mammals, but despite extensive research, evidence for differential maternal energy expenditure between sexes remains equivocal (Goldsworthy 1995, Ono and Boness 1996, Lunn and Arnould 1997, Guinet et al. 1999). Female AFS (Arnould et al. 1996*a*) and California sea lion (*Zalophus californianus* (Lesson, 1828)) pups (Luque and Aurioles-Gamboa 2001), have higher lipid stores than male pups, so the use of maternal resources should be studied in greater detail to clarify this issue. However, while male and female AFS pups appear to grow at the same rate in South Georgia (Lunn and Arnould 1997), males grow faster than females at Macquarie and Heard Islands (Goldsworthy 1995, Guinet et al. 1999). Therefore, the factors that influence intersexual differences in mass gain and loss throughout lactation are not yet clear, and should be considered in comparisons of maternal strategies between species.

One of the advantages of using otariids as a model for studies of maternal strategies is the large variation in lactation duration. For example, Northern (*Callorhinus ursinus* (L., 1758)), South American (*Arctocephalus australis* (Zimmermann, 1783)), and Antarctic fur seals, which breed at high latitudes in highly productive waters, but with large seasonal fluctuations, have brief lactation periods lasting approximately 4 mo. In contrast, Galapagos fur seals (*Arctocephalus galapagoensis* (Heller, 1904)), which breed in less productive and less seasonal environments, but with high inter-annual variability, have extended lactation periods which may last up to three years (Trillmich 1990, Gales and Costa 1997). Species breeding in more temperate latitudes, such as New Zealand (*A. forsteri* (Lesson, 1828)), Juan Fernandez (*A. philippi* (Peters, 1866)), Guadalupe (*A. townsendi* (Merriam, 1897)), South African (*Arctocephalus pusillus pusillus* (Schreber, 1775)) and South Australian (*A. pusillus doriferus*, and subantarctic (*A. tropicalis* (Gray, 1872)) fur seals, have lactation periods of intermediate length (10 months).

Both Northern and Antarctic fur seals have a relatively rigid lactation duration (4.5 mo), irrespective of breeding location. Such an inflexible lactation duration may be beneficial in high latitudes, where food availability shows high seasonal, but low interannual, variation in food abundance. However, a brief lactation period may not be optimal at lower latitudes, where food availability shows less seasonal, but higher interannual, variation. A flexible lactation duration may help animals cope with such high interannual variation in food supply by allowing females to adjust the amount of maternal expenditure over a longer period. Pups that survived the first few months of life may thus increase their chances of survival during years of low food abundance by foraging on their own and consuming milk from their mothers. In species with brief lactations, pups may have to grow as fast as possible before weaning and thereafter rely exclusively on their developing foraging abilities. Their energy demands during this period are particularly high and growth is near maximum values (Baker et al. 1994, Gentry 1998). These pups wean in fall, when prey availability decreases towards the annual winter minimum and may experience greater mortality than pups that can suckle during this time. In fact, Guinet et al. (1994) found that, in Iles Crozet, interannual changes in pup production were negatively correlated with El Niño events in Antarctic but not in subantarctic fur seals.

In addition to lactation duration, previous studies have examined diet (e.g. Daneri and Coria 1992, Reid and Arnould 1996), diving behaviour (Gentry and Kooyman 1986*a*), at-sea distribution (Goebel et al. 1991, Francis et al. 1998, Bonadonna et al. 2000), as well as the characteristics of maternal care, such as time spent on shore and at sea, and time spent suckling (Trillmich 1990, Goldsworthy 1999) of fur seals. However, inter- and intraspecific differences in these components of maternal strategy are strongly affected by spatiotemporal variations in the distribution and general ecology of prey species, which may be more important determinants of these strategies than environmental seasonality (Arntz et al. 1991, Francis et al. 1998, Gentry 1998). Comparative studies seeking to determine the factors involved in the evolution of different lactation strategies have been constrained by the inability to control for different environmental conditions across the range of the species studied.

AFS and SFSs breed sympatrically at 3 subantarctic islands: Marion Island, Iles Crozet, and Macquarie Island (Figure 1.3), where their populations are increasing rapidly (Guinet et al. 1994). These sites are at the southern and northern limits of the distributions of SFS and AFS, respectively, and are closely associated with the Subantarctic Front (SAF) (Figure 1.3). Therefore, the oceanographic habitat and seasonal changes in the environment at these sites are not the same as those at the core of each species' distribution (Antarctic Polar Front for AFS; Subtropical Front for SFS). No major differences in the diving behaviour and diet were found among both species at Macquarie Island (Goldsworthy et al. 1997). However, contrasting interspecific differences in the duration of lactation are observed between allopatric and sympatric populations. Sympatrically breeding AFS and SFS are, thus, a useful system for the study of maternal and pup growth strategies in relation to the environment.

1.3 Study site

My research was conducted at La Mare aux Elephants (MAE; 46°22'29" S, 51°40'13" E), at the western end of Ile de la Possession, during 2001-02 (December 4th - March 25th) and 2002-03 (December 1st - March 16th) breeding seasons (2001 and 2002 hereafter). La Mare aux Elephants (MAE) consists of two adjacent AFS and SFS colonies, which are on different types of substrate (Figure 1.6). AFS used the northern part of the beach, composed of small- to medium-sized pebbles, with gentle slopes behind; while SFS used the southern part of the beach, composed of large boulders eroded from the steep hinterlands. Both species gave birth close to shore, but the AFS colony grew in size as the season progressed, while the other species tended to remain close to shore during the same period. From late January through mid-March, the AFS colony spread to occupy most of the tussock area on the site, including the plateau on Figure 1.6a.

1.4 Natural history of Iles Crozet and Southern Indian Ocean

Iles Crozet are of volcanic origin and most of the coasts are rocky with little vegetation. On land, average minimum and maximum air temperatures range from 1°to about 11°C throughout the year, respectively, with precipitation being relatively high and roughly constant throughout the same period. On average, there are 300 rainy days per year and winds are strong on any given day, frequently reaching 75 km/h.

The Crozet archipelago lies near the northern limit of the Antarctic Circumpolar Current (ACC) in the Southern Ocean, which comprises the southern portions of the Atlantic, Pacific, and Indian oceans. In the Southern Indian Ocean sector, the structure of the ACC is strongly modified by the general topography of the seafloor, which affects the relative position of the major fronts that are associated with this current (Park et al. 1993, Sparrow et al. 1996). These fronts play an important role in the ecosystem, as they influence the distribution and abundance of organisms across trophic levels (Lutjeharms et al. 1985, Koubbi 1993, Bost et al. 1997, Guinet et al. 1997, Pakhomov and Froneman 2000). Seabirds and marine mammals tend to concentrate their foraging effort in and around such fronts. Therefore, knowledge of the main properties of oceanic fronts, as well as their temporal shifts, is useful to understanding community structure and predator behaviour.

1.4.1 Oceanography

Sparrow et al. (1996) described the major fronts that can be identified in the Indian Ocean sector of the Southern Ocean as follows (from north to south): i) the Agulhas Return Front (ARF), with temperature changes from 12° to 16°C at 200 m depth, ii) the Subtropical Front (STF), with temperature changes from 10° to 12°C at 100 m, iii) the SAF, characterized by the rapid descent of a salinity minimum below about 300 m, iv) the Antarctic Polar Front (APF), which has a surface (maximum gradient of sea surface temperature (SST) between 2° and 6°C) and a subsurface (northern limit of the 2°C isotherm below 200 m) expression, and finally The area formed between the APF and the SAF is known as the Polar Frontal Zone (PFZ), and this is where Iles Crozet are located. Similarly, the area between the STF and the SAF is also known as the Transition Frontal Zone (TFZ), and where the ARF, STF, and SAF merge, is also known as the Crozet Front (CF). Current velocities in the CF are among the strongest in the world, accounting for most of the horizontal transport of the ACC. As a result of the merging of the ARF, STF, and SAF at 40°E, the PFZ is unusually wide between 40°E and 60°E.

Although the structure of Southern Ocean fronts is clearer below the surface, their positions can be reasonably inferred from sea surface temperatures values in the Crozet region (Anilkumar et al. 2006). Thus, the 18.4°C, 12.5°C, 8°C, and 4.5°C isotherms APF (Park and Gamberoni 1997) correspond well to the ARF, STF, SAF, and APF, respectively. The association of surface temperatures with fronts is strongest in summer due to the higher stability of the water column compared with winter. The southern portion of the PFZ, particularly the APF, is extensively used by king penguins and other seabirds, as well as Antarctic fur seals, while foraging for myctophid fish and cephalopods (Stahl et al. 1985, Bost et al. 1997, Green 1997, Bonadonna et al. 2000). Fronts are areas of enhanced productivity due to strong mixing by currents and eddies, which increase the availability of nutrients for phytoplankton growth, so prey may be more abundant or available for predators at higher trophic levels (Lutjeharms et al. 1985).

Southern Ocean fronts display marked seasonal changes, as shown by seasonal composite images of SST satellite data of the Southern Indian Ocean sector from 2002 to 2008 (Figure 1.5). Unlike the oceanographic habitat for SFSs at Amsterdam or Gough Islands, the STF does not undergo large latitudinal movements throughout the year. Instead, relatively large fluctuations are observed in the positions of the SAF and APF, with both fronts getting compressed against the STF during winter and expanding south during summer. A characteristic feature of this region is the reduced distance between the SAF and STF north of Iles Crozet, making it difficult to distinguish the ARF, STF, and SAF, which may run together in this region in their roughly southward trajectory of this group of fronts east of Iles Crozet. The permanent, topographically induced, northward intrusion of the PFZ between the Crozet plateau that surrounds the archipelago and the Del Cano rise to the west of it has a strong influence on the dynamics of phytoplankton growth and ecosystem consumers (Read and Pollard 1993). Therefore, the marine ecosystem around Iles Crozet presents conditions that may not be typical for both AFS and SFS.

1.4.2 Fish and squid: the major prey of sea mammals and birds

Ichthyoplankton and mesopelagic fish assemblages closely follow the spatial structure of the Southern Indian Ocean. For example, the ichthyoplankton and mesopelagic fish assemblages in the PFZ can be clearly distinguished from those found in the adjacent subantarctic and polar areas (Koubbi 1993). Due to the large size of the PFZ around the Crozet Islands, the fish assemblages of Crozet and kerguelen do not differ substantially (Duhamel 1997). The main difference between these archipelagos is the absence of the fish family Channichthyidae in the neritic environment around the first archipelago, which may be due to its narrower shelf. Mid-water fish assemblages are, however, essentially the same in both Crozet and Kerguelen, coinciding with the location of both archipelagos in the PFZ. Some of these species have been classified by Koubbi (1993) into 5 categories, according to their distribution in relation to oceanic fronts: i) exclusively subtropical taxa, ii) taxa found between the SAF and

ARF, iii) taxa found in the STF and south to the SAF, iv) taxa occurring only in the PFZ, and v) Antarctic taxa and demersal species of the Kerguelen shelf. Table 1 shows a list of the species of fish found around Iles Crozet and their affinity for oceanic fronts, as studied in Koubbi (1993) and Duhamel (1997).

In addition to the vertical distribution and abundance, the ichthyofauna around the subantarctic islands also shows marked diel variation in these characteristics. For instance, in waters surrounding Iles Kerguelen (Duhamel et al. 2000), 3 species (*Lepidonotothen squamifrons* (Günther, 1880), *Muraenolepis marmoratus* (Günther, 1880), and *Krefftichthys anderssoni* (Lönnberg, 1905)) dominated the upper 150 m of the ocean during the day, with 2 being found exclusively in the peri-insular shelf. All of them, except *K. anderssoni*, were early life stages of benthic fish and only *M. marmoratus* were large enough to be considered potential prey for king penguins. Seven other myctophids were found in deeper layers (250 m and 300 m) during this time. During the night, both abundance for most species and species diversity were higher (Duhamel 1998, Duhamel et al. 2000). Five of the myctophids found in deep water during the day became dominant in the upper 100 m during the night, being joined by *Gymnoscopelus braueri* (Lönnberg, 1905), *Electrona subaspera* (Günther, 1864), and *G. piabilis* (Whitley, 1931). These species, together with *E. antarctica* (Günther, 1878), *G. nicholsi* (Gilbert, 1911), and *Protomyctophum tenisoni* (Norman, 1930), tended to concentrate near the surface at night, while *P. andriashevi* (Becker, 1963), *K. anderssoni*, *G. bolini* (Andriashev, 1962) and *E. carlsbergi* (Tåning, 1932), never reached the surface. Furthermore, the composition of the catches varied with distance to the shore, such that *E. carlsbergi* and *P. andriashevi* dominated close to the shelf, but were progressively replaced by *K. anderssoni* and, farthest from shore, by *B. tenuis* (Kobyliansky, 1986). It is interesting to note that all of these species are typical of the PFZ in the Indian Ocean and are also present around the Crozet

Archipelago, to the west of Kerguelen. Therefore, a similar pattern should be found in the former group of islands, although some differences are expected, as the shelf is much broader in Iles Kerguelen.

The fish diet of several seabirds and marine mammals from the Keguelen-Heard Plateau has been investigated in some detail, mostly at Heard Island (Green et al. 1989, Klages et al. 1990, Woehler and Green 1992, Cherel et al. 1997, Green et al. 1997). All of these predators consumed mainly myctophids (most importantly *G. nicholsi*, *G. piabilis*, and *K. anderssoni*), but some included the Channichthyid *Champsocephalus gunnari* (Lönnberg, 1905) as an important prey item during the summer (Green et al. 1998). The bentho-pelagic *C. gunnari* inhabits shelf waters in the Kerguelen-Heard Plateau, and it must represent a profitable resource for predators during the summer, when they are constrained by the fasting abilities of their chicks or pups on land.

Consistent with the conclusions of Duhamel (1997), *C. gunnari* has never been found in the diet of king penguins from the Crozet Islands (Cherel and Ridoux 1992, Bost et al. 1997). No information is available from other predators in this archipelago. Three myctophid fish dominated the diet of king penguins during the summer: *K. anderssoni*, *E. carlsbergi*, and *P. tenisoni*, with the first one being the most abundant. Penguins, however, seem to forage for these species near the APF, particularly at its northern limit, or, to a lesser extent, near the southern limit of the SAF (Guinet et al. 1997, Moore et al. 1999*a*). During the summer, myctophids appear to be more abundant and closer to the surface during the night in the SAF than in the APF (Pakhomov et al. 1994). Both fronts are at approximately the same distance from the Crozet Islands, typically far from the islands' shelves. It is interesting to note that the three myctophids on which penguins predominantly feed are truly oceanic and, at least *K. anderssoni*, seems to be most abundant away from island shelves (Perissinotto and McQuaid 1992). Data from other seabirds breeding in Crozet also indicate the importance of myctophids in their diets, although some consume cephalopods and crustaceans to a lower extent (Ridoux 1994, Catard et al. 2000).

At least 7 cephalopod families are known to occur around Iles Crozet (Cherel et al. 1996). Based on diet analyses of king penguins and wandering albatrosses feeding in this region, (Cherel and Weimerskirch 1999) found that the onychoteuthid squids *Kondakovia longimana* (Filippova, 1972), *Moroteuthis ingens* (Smith, 1881), and *M. knipovitchi* (Filippova, 1972) are abundant, and that the first two spawn in winter near the islands. According to the recent Atlas of cephalopod distribution in the Southern Ocean (Xavier et al. 1999), which shows the distribution of squids in relation to oceanic fronts, there are 8 species that could potentially be found around Crozet, in addition to the 9 identified by Cherel et al. (1996) in king penguin diet. Some of these cephalopods, particularly the onychoteuthids, feed on myctophid fish and smaller invertebrates, including euphausid crustaceans, decapods, amphipods, and chaetognaths.

1.4.3 Seabirds

There are 36 species of seabirds breeding in Iles Crozet, some of which have their largest populations in these islands, making the islands' avifauna the richest in the world when diversity and abundance are combined. Of these, the most abundant are macaroni and king penguins, with populations of 6 x 106 and 2 x 106 individuals, respectively (Guinet et al. 1996). King and macaroni penguins, and along with elephant and fur seals are the principal marine predators consuming 56% of the prey eaten by the whole land-based community of Iles Crozet (Guinet et al. 1996). All of these predators consume mostly myctophid fish, cephalopods, and crustaceans.

The large amount of resources used by these predators is likely to result in considerable ecological segregation between closely related species. The broad geographic patterns in the distribution of the ichthyofauna in relation to oceanic fronts could exert a strong influence on the foraging strategies of marine predators and for ecological segregation among them. Understanding the mechanisms that control how these species divide their resources should help predict how they might be affected by natural or anthropogenic disturbances in their ecosystem.

Concurrent studies of the spatial and dietary segregation of seabirds from the Iles Crozet are lacking, but independent analyses suggest that foraging area and timing of breeding may be the most important variables determining the extent of ecological segregation among seabirds from Iles Crozet (Stahl et al. 1985, Ridoux 1994). There are 4 species that feed close to shore (*Phalocrocorax atriceps* (King, 1828), *Larus dominicanus* (Lichtenstein, 1823), *Sterna virgata* (Cabanis, 1875), and *S. vittata* (Gmelin, 1789)), while the rest of the species forage either over shelf areas or near oceanic fronts (Stahl et al. 1985). However, the extent of spatial habitat segregation among seabirds is apparently larger during the winter than during the summer. Although dietary differences may not be as important as spatial habitat differences, it is possible to distinguish the diet composition and prey size distribution of diving (penguins, diving petrels, and cormorant) from the surface feeding (albatrosses, petrels, and storm petrels) (Ridoux 1994). Dietary overlap indices appear to be higher and prey size distributions narrower among the former group than among the latter. Diving may allow some seabirds to access more abundant resources below the surface during a period of reduced productivity, thereby minimizing competition and thus the pressure to partition their niche along these dimensions (Pianka 1978).

1.4.4 Pinnipeds

Iles Crozet fosters a population of approximately 3,400 elephant seals (*Mirounga leonina* (L., 1758)), 500 AFS, and 1,000 SFS. However, elephant seals have a reproductive strategy which differs markedly from the smaller fur seals inhabiting the islands. Pregnant elephant seal mothers forage over vast areas of the Southern Ocean during most of the year (Jonker and Bester 1998) and then return to the colony in late August to give birth and nurse their pup for about 25 days, during which they fast. All adult females are absent from the colony by the end of November, but there is another other peak in abundance occurring in late January corresponding to the molt, while a few juveniles can be found hauled out during the rest of the year. At the individual level however, elephant seals stay on land for only 1 or 2 months in any given year. This contrasts sharply with fur seals, which congregate on land to breed from mid-November to late January, so there is a temporal segregation of phocid and otariid niches. Furthermore, female fur seals regularly forage during the whole lactation period, which lasts 4 and 10 months in Antarctic and subantarctic fur seals, respectively. Elephant seals from nearby Heard Island (southeast of Crozet) (Slip 1995) feed mostly on cephalopods, but also consume fish, including myctophids, which they probably catch at depths of more than 300 m (Jonker and Bester 1998), much greater than that used by foraging fur seals.

There are 3 species of fur seal that inhabit areas under the influence of the APF: the New Zealand, subantarctic, and Antarctic fur seals. All other otariids breed north of the APF. The first of these species is found in Macquarie Island, but also has other populations in the southern coast of Australia and islands south of New Zealand. The latter two are circumpolar in distribution and can be found in several subantarctic islands (Figure 1.3). All of them were, to differing degrees, subject to exploitation during the 18th nd 19th. Sealing was mostly associated with whaling operations and the exploitation of elephant seals, which took place at the more southerly locations. Because Antarctic fur seals are the only ones breeding mostly south of the APF, where sealers and whalers focused their activities, they were more negatively affected by sealing than other fur seals. Subantarctic and New Zealand fur seals breed on islands north of the APF, where few or smaller populations of elephant seals were found, so their numbers were not so severely affected during this period.

Based on these observations, Wynen et al. (2000) postulated that subantarctic fur seals should have higher levels of genetic diversity than Antarctic fur seals. Present populations of Antarctic fur seals, on the other hand, may have arisen from a few individuals that survived the sealing period. Testing this hypothesis, Wynen et al. (2000) found that subantarctic fur seals have higher levels of population structure than Antarctic fur seals. The lower levels population structure in the latter species is thought to result from individuals immigrating from a few source populations. However, Wynen et al. (2000) concluded that Antarctic fur seals may be divided into a western region (South Georgia, South Shetland, Bouvetøya, Marion, and Heard Islands), and an eastern region (Kerguelen and Macquarie). South Georgia and Bouvetøya were the probable source populations for most of the western region. In the case of subantarctic fur seals, Macquarie and Crozet Islands were probably colonized by animals from Marion Island, and to a lesser extent, from Amsterdam Island.

Besides the conspicuous difference in lactation length between the fur seals, no studies have been conducted in Iles Crozet to investigate the extent of ecological segregation between them. There is a slight difference in the timing of births, with the peak of AFS pup births occurring around 5 December, while that of SFS pups is around 15 December. The reasons for this difference are not yet clear, but given the difference in the duration of lactation, it may be more significant for AFSs because it represents a larger fraction of the total lactation period.

The most abundant of all southern fur seals is the Antarctic fur seal, which numbers at least 2 million individuals (Bonner 1999). Subantarctic fur seals are the next most numerous, with approximately 300,000 individuals, while New Zealand fur seals are the least abundant, with about 55,000 animals. Subantarctic fur seals are far more numerous than the Antarctic species where they breed sympatrically (Marion, Macquarie, and Crozet Islands). There are approximately 1,500 and 74,000 Antarctic and subantarctic fur seals in the Prince Edward Islands (Hofmeyr et al. 1997), 500 and 1,000 at Iles Crozet (extrapolated from data in Guinet et al. (1994) assuming equal age/sex structure as at Prince Edward Islands), and at least 111 and 42, respectively, in Macquarie Island (Goldsworthy et al. 1999). Conversely, Antarctic fur seals are much more abundant at breeding localities south of the PF, such as South Georgia and the South Shetland Islands (Boyd 1993, Croll and Tershy 1998), where subantarctic fur seals do not breed. Southeast of the Crozet Islands, (Goldsworthy and Shaughnessy 1989) reported 13 subantarctic fur seals (including a pup) in Heard Island, compared with about 15,000 Antarctic fur seals hauling out there (Shaughnessy et al. 1998), although the development of a breeding colony of the first species has not been documented thereafter. This represents the farthest south of the PF subantarctic fur seals are known to breed.

The populations of both fur seal species have been increasing at a rate of approximately 16% per annum in the Crozet Islands, which represents one of the highest growth rates reported for any otariid species (Guinet et al. 1994). Therefore, it is expected that fur seal numbers in 2001 will be higher than those listed above.

1.5 Objectives and thesis structure

In this dissertation, I investigated interspecific differences in: i) the foraging ecology of lactating females, ii) the allocation of maternal resources into their pups, and iii) the use of maternal resources by pups as they approach weaning between sympatrically breeding Antarctic and subantarctic fur seals at Ile de la Possession, Iles Crozet, Southern Indian Ocean. I examined inter-relationships among these components of the maternal strategy, pup growth and development. I asked: what aspects of maternal and pup growth strategies are more flexible, and which aspects may be more rigid adaptations to the APF or SAF, that broadly define each species' worldwide distribution (AFS and SFS, respectively)? I also considered the implications of the answer to this question to the extent of ecological segregation between the two species at Iles Crozet.

My thesis consists of four data chapters, divided into two parts, preceded by the general introduction presented above. Part I contains two major chapters, where I compare the major aspects of foraging behaviour of lactating females (Chapter 2), followed by a more detailed analysis of diving behaviour to resolve what mechanisms might be driving differences at the coarser scale (Chapter 3). Proper identification of the temporal and spatial scales at which a diving forager perceives the environment relies heavily on how accurately, and objectively, diving behaviour can be grouped into natural "bouts" representing those scales. I begin Chapter 3, therefore, with a technical section describing an objective and accurate method for identifying bouts of diving behaviour that builds upon previous research. In the following section, I present evidence to argue that lactating SFS females have greater aerobic dive limit, and that it affects the scales at which they forage. Appendix A describes characteristics of a software package I wrote to perform the analyses in Part I. Appendix B is a related paper I contributed to, where foraging locations and general descriptions of diving behaviour are compared between AFS and SFS, complementing Chapter 2.

In Part II, I compare the growth of pups from birth to 100 days of age, representing almost the entire lactation period of AFS and one half of that of SFS (Chapter 4). Numerous studies have described body mass and body length growth in AFS and SFS at allopatric sites, but none (to the best of my knowledge) have done so using a comprehensive set of morphometric variables to document the process of physical maturation prior to weaning. In Chapter 4, therefore, I compare growth and allometry for several morphological traits to argue that AFS pups mature more rapidly, in preparation for weaning at a younger age. In Chapter 5, I link the maternal strategies described and compared in Part I with pup development, examining the dynamics of mass changes during maternal foraging cycles and pup body composition in more detail. My goal here was to determine whether relative milk intake differed between species, and whether pups use energy differently to account for the observed growth patterns. Appendix C is a related paper I contributed to, where pup metabolism is compared between species, complementing Chapter 5.

I conclude with Part III, where I synthesize the key results from each chapter in terms of my thesis objectives, and discuss how they contribute to our understanding of otariid maternal care strategies.

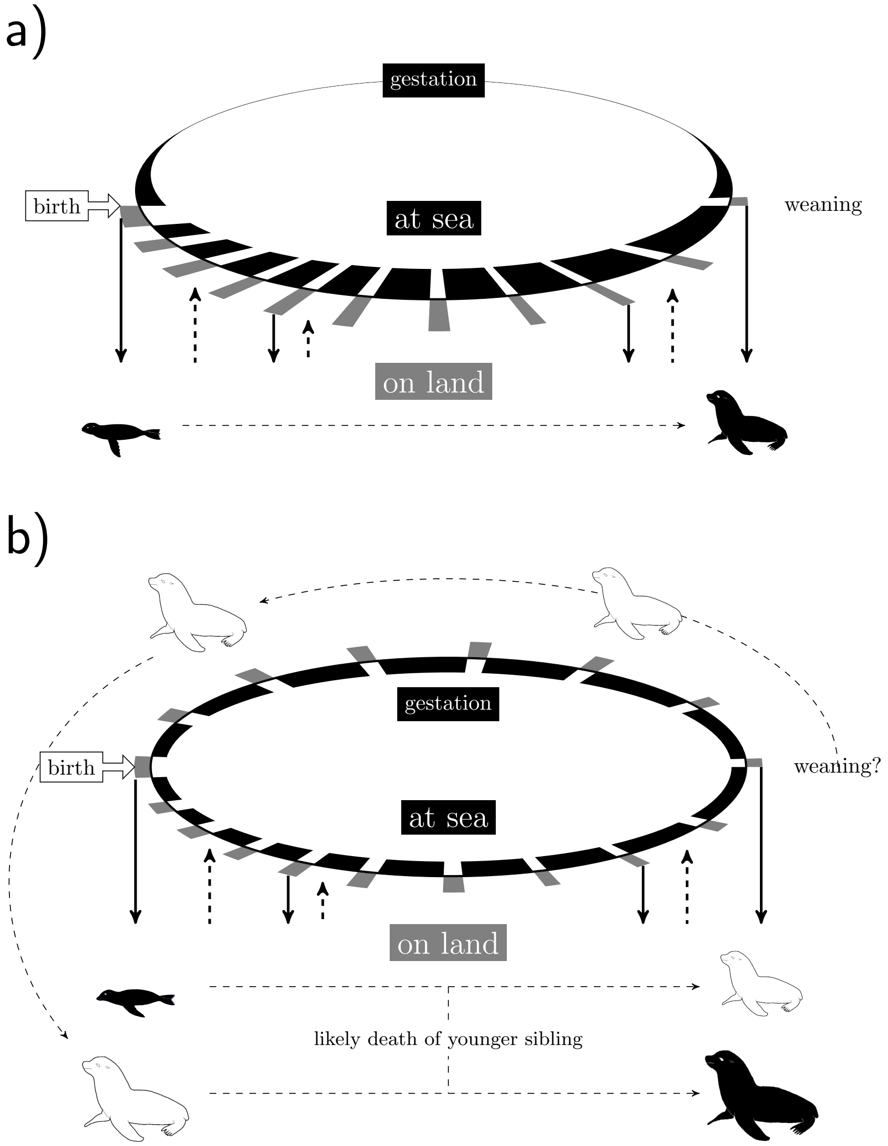

Figure 1.1. a) In otariid species with brief lactations (e.g. Northern and Antarctic fur seals), females nurse their pup during summer and early autumn, and pups are weaned in late autumn or winter. b) In species with long lactations (e.g. Galapagos fur seals and sea lions), pups may not be weaned before the female gives birth on her next reproductive cycle, establishing competition between siblings for maternal resources, which the younger one has a greater chance of losing. Lactating females perform regular foraging trips (black rectangles) to sea, returning to shore to nurse their pup (gray rectangles). Their pups gain mass while she is ashore nursing (solid arrows) and partly lose it when she is at sea (upward dashed arrows). Modified after (Bonner 1984)

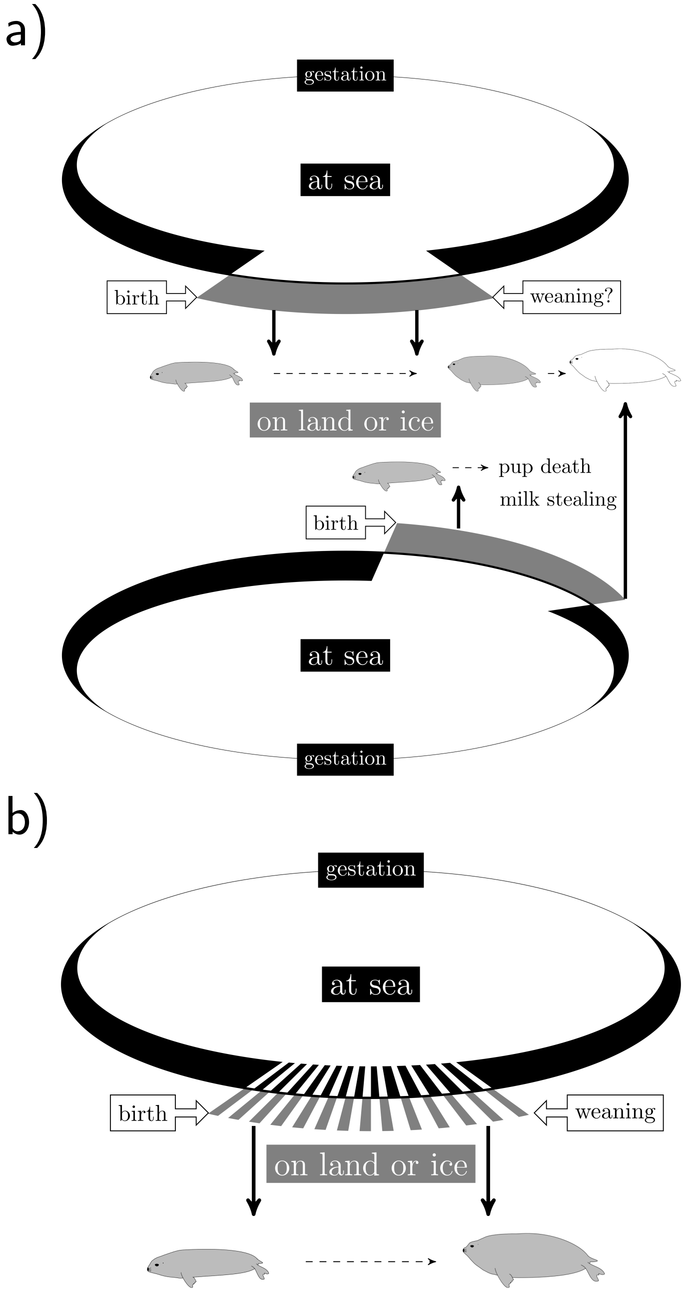

Figure 1.2. Phocid pinnipeds are, in general, larger than otariids, and in a) the largest species (e.g. elephant and hooded seals), mothers can build up and store most of the energy needed for lactation during a prolonged "foraging" trip that lasts most of their reproductive cycle. In this case, mothers can remain ashore, fasting, for the entire duration of lactation, which is briefer than that of otariids. Some pups are able to marginally prolong lactation by stealing milk from a female whose pup has died. However, in b) the smallest species (e.g. harbour and ringed seals), females cannot afford this strategy and, therefore, require frequent foraging to sustain the costs of lactation, especially in late lactation. This strategy is reminiscent of that observed in otariids, although lactation remains considerably briefer in phocids, and pups are weaned in late spring. The meaning of symbols is as in Figure 1.1

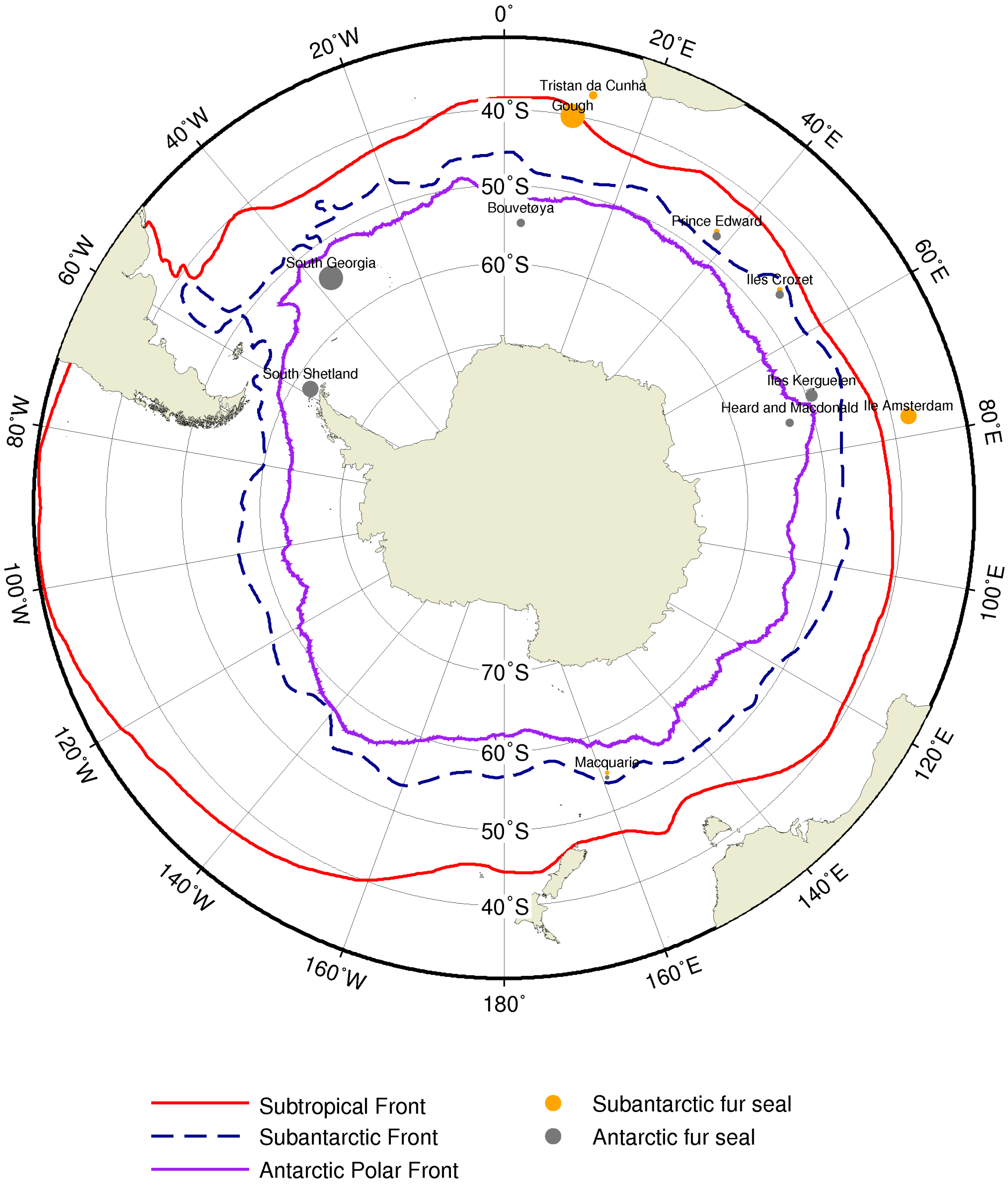

Figure 1.3. Distribution of Antarctic (AFS) and subantarctic fur seal (SFS) breeding colonies in relation to average position of Southern Ocean fronts (Orsi et al. 1995, Moore et al. 1999*b*). The size of the symbols is proportional to the fraction of the total estimated population of each species at each locality

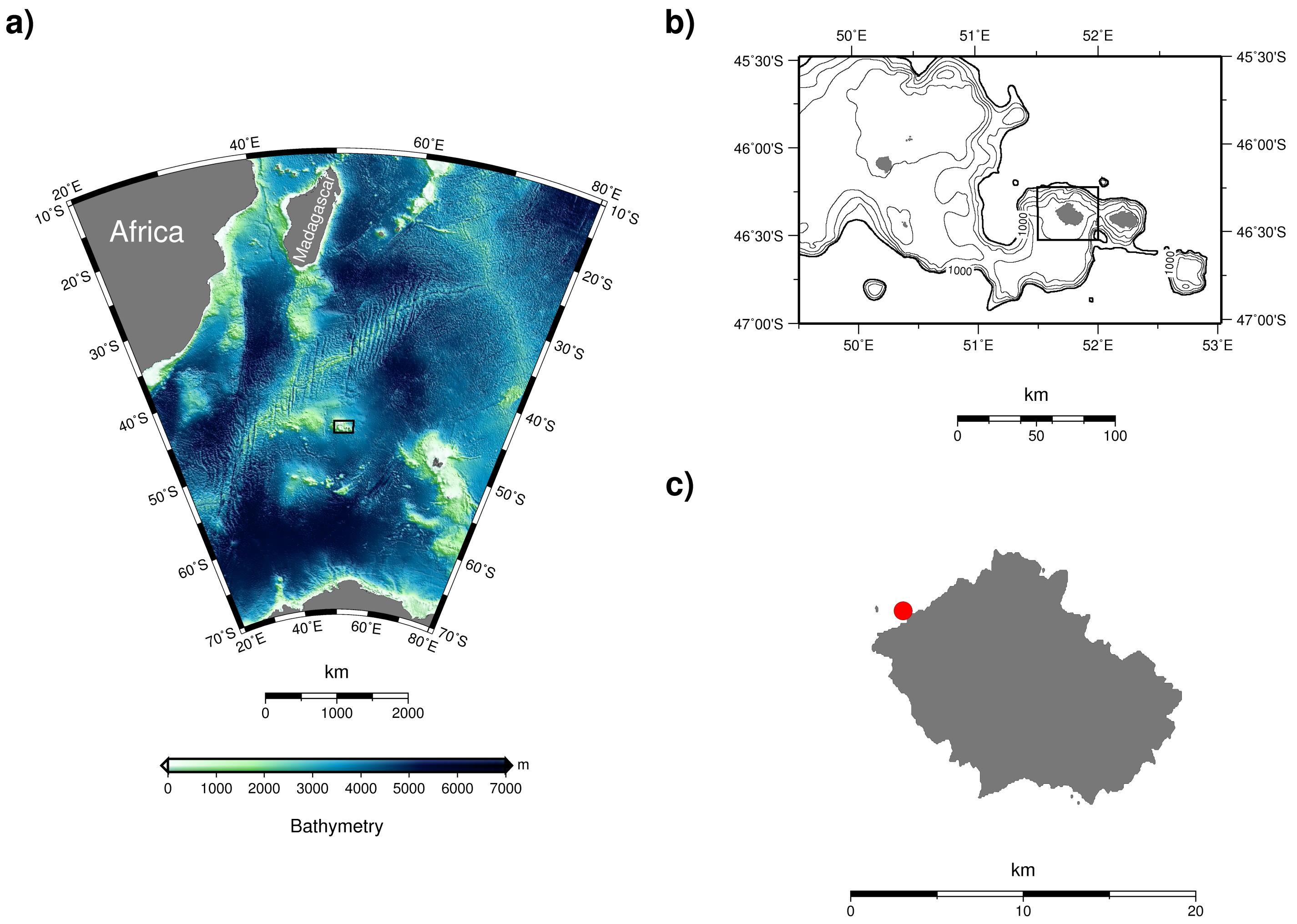

Figure 1.4. a) Location of Iles Crozet in the Southern Indian Ocean and surrounding bathymetry. b) Bathymetry in the vicinity of Iles Crozet showing steep gradients close to the islands (isobaths between 200 and 1000 m, at 200 m intervals, are shown as black lines). c) La Mare aux Elephants, at the western end of Ile de la Possession (red circle), was chosen as study site

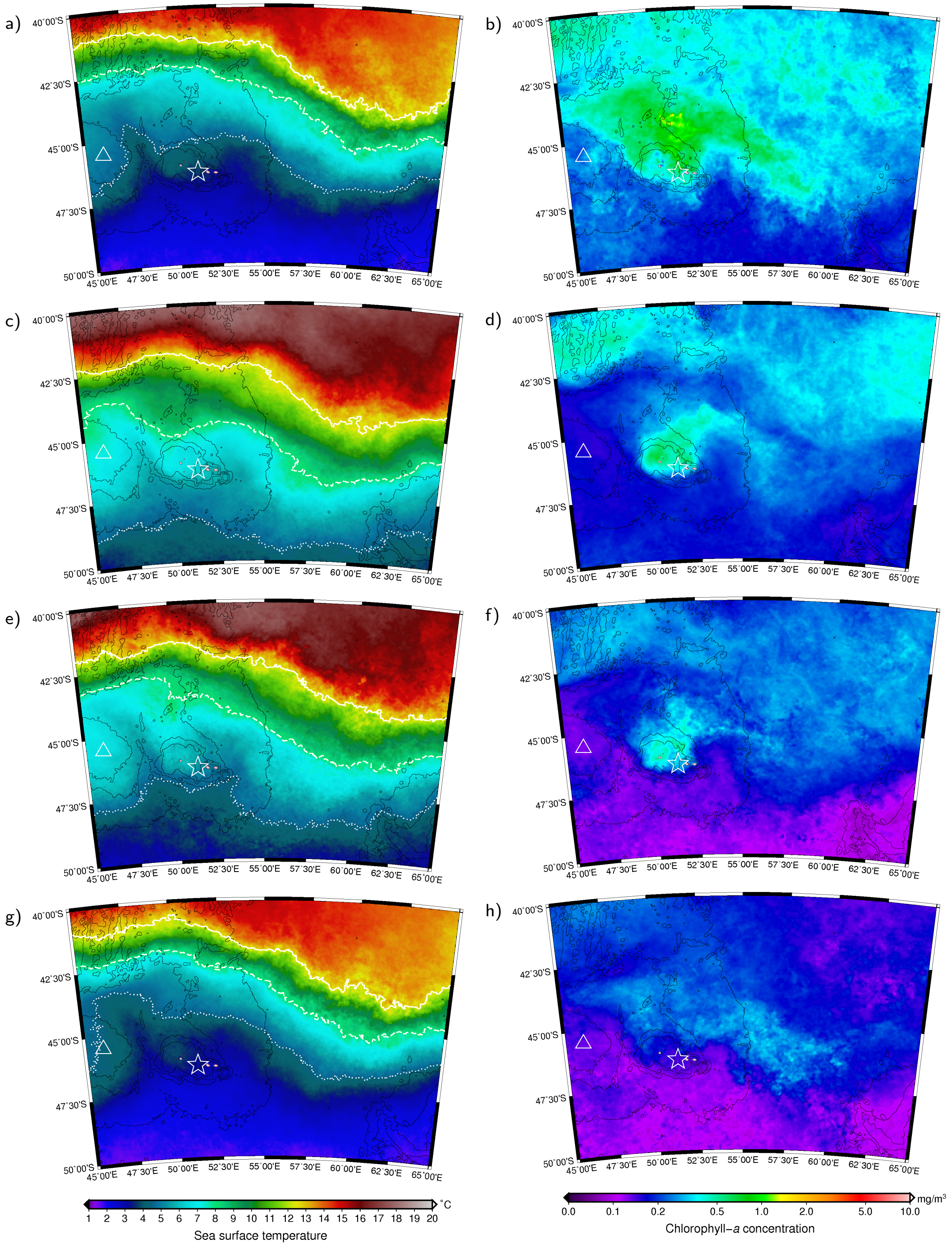

Figure 1.5. Seasonal composite (2002 to 2008) of sea surface temperature structure of ocean fronts (left panels) and chlorophyll *a* concentration (right panels) around Iles Crozet, as observed via MODIS Aqua satellite during spring (a, b), summer (c, d), autumn (e, f), and winter (g, h). The 1000, 2000, 3000, and 4000 m isobaths are shown as thin black solid lines. From north to south: Subtropical Front (solid white line), Subantarctic Front (dashed white line), and Antarctic Polar Front (dotted white line). Note the persistent northward intrusion of the Polar Frontal Zone between the Crozet plateau around the archipelago (white star) and the Del Cano rise (white triangle) to the west of it

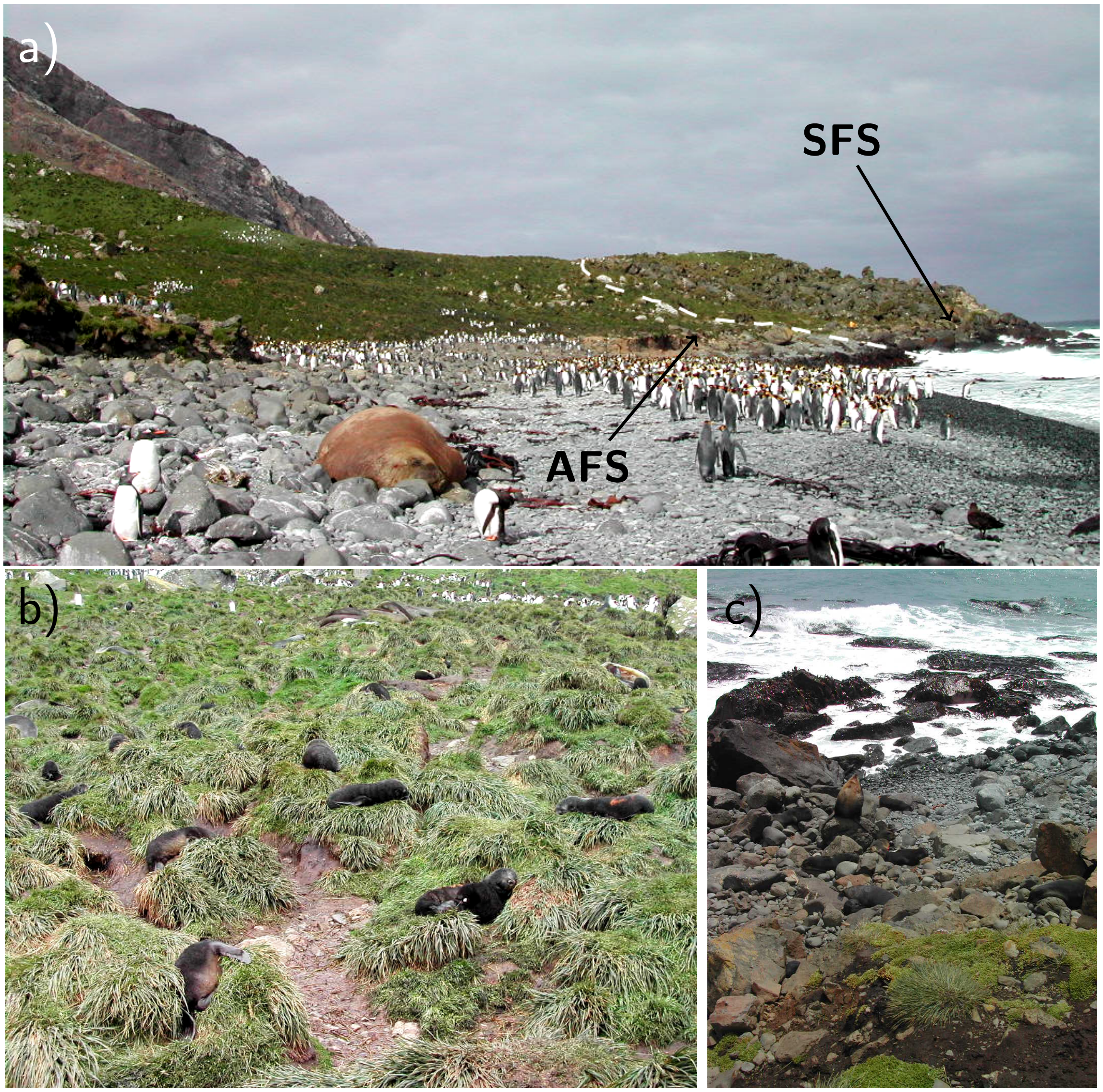

Figure 1.6. Study site (La Mare aux Elephants) at the western end of Ile de la Possession, Iles Crozet. a) Zones where Antarctic (AFS) and subantarctic (SFS) fur seals were concentrated during the birth period and early lactation are indicated by the solid arrows. The dashed white line separates the colonies of each species. Nursing females and their pups spread over larger areas throughout lactation, with AFS occupying the much wider area inland up to the plateau and hills (upper left) with tussock, and SFS spreading to a much smaller area within the rocky and bouldery zone just inland from the birth zone. b) The typical tussock zone where AFS females nursed their pups. c) The typical rocky, bouldery, zone where SFS females nursed their pups

Part I

Maternal strategies

Chapter 2

Foraging behaviour of sympatric Antarctic and subantarctic fur seals: does their contrasting duration of lactation make a difference?

Abstract

The duration of periods spent ashore vs. foraging at sea, diving behaviour, and diet of lactating female Antarctic (*Arctocephalus gazella* (Peters, 1875), AFS) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872), SFS) fur seals were compared at Iles Crozet, where both species coexist. The large disparity in lactation duration (SFS: 10 mo, AFS: 4 mo), even under local sympatry, has led to the expectation that AFS should exhibit higher foraging effort or efficiency per unit time than SFS to allow them to wean their pups in a shorter period of time. Previous evidence, however, has not supported these expectations. In this study, the distribution of foraging trip durations revealed two types of trips: overnight (OFT, < 1 d) and long (LFT, > 1 d), in common with other results from Macquarie Island. However, diving behaviour differed significantly between foraging trip types, with greater diving effort in OFTs than in LFTs, and diving behaviour differed between fur seal species. OFTs were more frequent in SFS (48%) than in AFS (28%). SFS performed longer

LFTs and maternal attendances than AFS, spending a smaller proportion of their foraging cycle at sea (66.2% vs. 77.5%, respectively). SFS dove deeper and for longer periods than AFS, in both OFTs and LFTs, although indices of diving effort were similar between species. Diel variation in diving behaviour was lower among SFS, which foraged at greater depths during most of the night time available than AFS. The diving behaviour of AFS suggests they followed the nychthemeral migration of their prey more closely. Concomitant with the differences in diving behaviour, AFS and SFS fed on the same prey species, but in different proportions of 3 myctophid fish (*Gymnoscopelus fraseri* (Fraser-Brunner, 1931), *G. piabilis*, and *G. nicholsi*) that represented most of their diet. The estimated size of the most important fish consumed did not vary significantly between fur seal species, suggesting that the difference in dive depth was mostly a result of changes in the relative abundance of these myctophids. The energy content of these fish at Iles Crozet may thus influence the amount and quality of milk delivered to pups of each fur seal species. These results contrast with those found at other sites where both species coexist, and revealed a scale of variation in foraging behaviour which did not affect their effort while at sea, but that may be a major determinant of foraging efficiency and, consequently, maternal investment.

2.1 Introduction

Temporospatial separation of foraging and breeding is a defining characteristic of pinnipeds, and may constrain their evolution (Costa 1991). Unlike most phocid seals, otariid (fur seals and sea lions) lactating females cannot fast for the entire period of lactation, as they are too small to store all the required energy (Boness and Bowen 1996). Therefore, they alternate their time at sea foraging, with visits ashore to nurse their pup. Otariid lactation varies in duration from 4 months (Antarctic

Arctocephalus gazella (Peters, 1875) and northern *Callorhinus ursinus* (L., 1758) fur seals) to 3 years (Galápagos fur seals *A. galapagoensis* (Heller, 1904)), and single foraging trips range from several hours to about 50 days in duration, depending on the species, stage of lactation, population, and location (Beauplet et al. 2004, Schulz 2004). Such large variation has prompted efforts to identify the proximate and ultimate factors that determine what particular strategy an otariid adopts.

Studies on temperate species have emphasized the importance of prey ecology and variability of the physical environment in relation to otariid maternal strategies. For example, Juan Fernández (*A. philippi* (Peters, 1866)) and subantarctic (*A. tropicalis* (Gray, 1872)) fur seals both have a 10-month lactation, during which lactating females feed on epipelagic fish (mean depths $<$ 30 m), mostly at night (Ochoa-Acuña and Francis 1995, Beauplet et al. 2004). Mean duration of foraging trips increases in both species from 1-2 d early in lactation, to 25-50 d just prior to weaning. In contrast, foraging trips of Australian fur seals (*Arctocephalus pusillus doriferus* (Wood Jones, 1925)) rarely exceed 10 d during lactation, and females feed at much greater depths on benthic prey at all times of day (Gales and Pemberton 1994, Arnould and Hindell 2001). These three species inhabit temperate latitudes with similar seasonal regimes, so differences among them have challenged an early hypothesis set forth to explain the variation in fur seal foraging behaviour, that presents environmental seasonality as the main determinant of interspecific differences in foraging-nursing cycles (Gentry et al. 1986).

A drawback of interspecific comparisons using samples from different locations is that environmental variation is usually unaccounted for. However, several examples of different species breeding on the same islands exist, offering the opportunity to control for this factor. Here we compare the foraging behaviour of sympatric Antarctic (*A. gazella*) and subantarctic (*A. tropicalis*) fur seals (AFS and SFS, respectively, hereafter), two phenotypically similar sister species with large differences in duration of lactation. AFS breed mainly on islands south of the Antarctic Polar Front, while SFS do so mainly on islands just north of it, but they breed sympatrically in 3 groups of islands: Macquarie Island, Iles Crozet, and the Prince Edward Islands (Bonner 1999). Lactation is 116 d long in AFS (Costa et al. 1988, Lunn et al. 1993) and 300 d long in SFS (Kerley 1987, Guinet and Georges 2000), and this trait appears to be constant throughout their distribution. SFS pups were shown to have lower energy requirements and higher body fat stores, compared to AFS pups (Arnould et al. 2003), even though rate of milk consumption was only slightly higher in AFS. Therefore, AFS females have <50% of the time that SFS females have for investing in their offspring, but their offspring's energy demands may be higher (Arnould et al. 2003). Understanding how individuals of these species forage when in sympatry, yet under such different pressures, can thus help reveal which elements of foraging behaviour are species-specific and relatively invariant, and which ones are plastic and adaptively responsive to environmental influences.

The foraging ecology of AFS and SFS has been studied thoroughly at various locations throughout their range, over several time scales. The diet of AFS varies geographically, with Antarctic krill (*Euphausia superba* (Dana, 1850)) being the main food resource in the southern Atlantic Ocean (South Georgia Doidge and Croxall 1985, Reid and Arnould 1996; Bouvetøya Kirkman et al. 2000), although fish complements their diet along the Antarctic peninsula (Casaux et al. 2003) and South Shetland Islands (Daneri 1996). In the southern Indian Ocean, fish is the main prey (Marion Island Klages and Bester 1998; Iles Kerguelen Lea et al. 2002*b*, and Heard Island Green et al. 1997). Based on scat analyses, SFS at Marion Island feed predominantly on myctophid fish (Klages and Bester 1998), but stomach content analyses suggest that at Marion (Ferreira and Bester 1999) and Gough (Bester and Laycock

1985) islands they feed mostly on cephalopods and on myctophid fish at Amsterdam Island (Beauplet et al. 2004). Some studies suggest that such intraspecific dietary differences are related to the analytical techniques used, but are also associated with differences in dive behaviour, both in terms of depth and diel activity patterns (AFS at South Georgia Croxall et al. 1985, Boyd and Croxall 1992; AFS at Iles Kerguelen Lea et al. 2002*c*, and SFS at Amsterdam Island Georges et al. 2000*b*).

If foraging behaviour is mainly determined by prey ecology, then dietarily similar sympatric fur seal species would be expected to differ little in foraging behaviour. At the level of entire foraging trips, this expectation has been supported in studies of AFS and SFS at Macquarie Island (Goldsworthy et al. 1997, Goldsworthy 1999, Robinson et al. 2002) and Iles Crozet (Bailleul et al. 2005). The species were similar in diet at Macquarie Island and exhibited similar foraging behaviour at both sites, with females diving close to the surface, mostly at night. Summer foraging areas of the species also overlapped considerably. Other data from Marion (Bester and Bartlett 1990, Kirkman et al. 2002, 2003) and Macquarie islands (Goldsworthy 1999) suggest no interspecific differences in the duration of foraging trips, except at Iles Crozet, where AFS made longer trips (Bester and Bartlett 1990, Robinson et al. 2002, Bailleul et al. 2005).

To date, comparisons of foraging behaviour of AFS and SFS have used the scale of the foraging trip (Bester and Bartlett 1990, Robinson et al. 2002, Kirkman et al. 2003, Bailleul et al. 2005). However, such a scale may not reveal ecologically important interspecific differences on finer scales. Night diving by fur seals is linked to the diel vertical migration of their prey (Croxall et al. 1985, Gentry 1998, Wells et al. 1999), so foraging behaviour optima are expected to show a diel pattern, particularly during the night (Mori 1998*a*). Therefore, important interspecific differences in the temporal distribution of dive effort and depth utilization may exist. Determining when and where the species concentrate their foraging effort in the water column, in relation to the prey they exploit, may reveal patterns that are related to their different lactation strategies. Moreover, the presence of overnight and longer foraging trips in both species at some locations raises the question of whether their functions differ. These questions have not been addressed, so the objectives of this study were to compare: (i) maternal attendance and foraging trip durations; (ii) diel patterns in diving, and how they vary between overnight and longer foraging trips; and (iii) diet of sympatric AFS and SFS at Iles Crozet. Because of their briefer lactation and the physiological differences between AFS and SFS pups outlined above, AFS females were expected to show briefer maternal attendance periods and foraging-trip durations. For the same reasons, they also were expected to spend greater effort while diving.

2.2 Materials and methods

2.2.1 Fur seal study colonies

Research was carried out at La Mare Aux Elephants (MAE; 46°22'29" S, 51°40'13" E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during 2001-02 (December 4th - March 25th) and 2002-03 (December 1st - March 16th) breeding seasons (2001 and 2002 hereafter). MAE consists of two adjacent AFS and SFS colonies, which are on different types of substrate. AFS used the northern part of the beach, composed of small- to medium-sized pebbles, with gentle slopes behind; while SFS used the southern part of the beach, composed of large boulders eroded from the steep hinterlands. Both species gave birth close to shore, but the AFS colony grew in size as the season progressed, while the other species tended to remain close to shore during the same period.

A total of 277 (AFS: 153, SFS: 124) pups were individually marked as previously described (Georges and Guinet 2000*a*, Arnould et al. 2003, Bailleul et al. 2005). Pup production and mean date of pupping were estimated using total pup counts (both years; including dead and living pups) on a weekly basis until no more births were observed. Peak pupping dates were 5 and 15 December (164 and 167 pups in 2001 and 2002, respectively) for AFS, and 25 and 30 December (80 and 91 pups in 2001 and 2002, respectively) for SFS. Therefore, there were inter-annual differences of up to 10 d, which suggests large environmental differences between study years (Lunn and Boyd 1993). However, Lunn and Boyd (1993) suggested that variation in pupping date at Bird Island, South Georgia, may reflect differences in environmental conditions during late gestation, rather than post-partum, which is our study period, so inter-annual differences in foraging behaviour were not fully analyzed. Populations of both species have been increasing at an annual rate of about 18%, at least until 1994 (Guinet et al. 1994).

2.2.2 Instrumentation, maternal attendance and diving behaviour

Animal capture and handling procedures were described in Bailleul et al. (2005). Briefly, lactating females of each species were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different time-depth recorder (TDR) models was glued to the dorsal fur between the scapulae, using a two-component glue (AW 2101 Ciba Specialty Chemicals): MK5, MK7, and MK8 (Wildlife Computers, Redmond, Washington, U.S.A.). There were no significant differences in foraging trip duration, dive depth, nor dive duration between animals instrumented with different TDR models ($P > 0.5$ in all cases), so data from the 3 models were pooled for interspecific comparison purposes. TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. The characteristics and composition of sampled females are summarized in Table 2.1. Instruments were left on the seals for 1 to 11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals' return to the colony.

TDR data were downloaded to a portable computer on the same day the instrument was recovered, to allow redeployment of TDRs on different individuals. Visualization and analyses of the resulting regular time series of dive data were performed using custom written software, available as GNU R (R development Core Team 2007) package diveMove (Luque 2007). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e. continuous depth readings) was available for at least 6 h. This limit was imposed to exclude short excursions to sea, for activities other than foraging, as these contained isolated shallow dives and mainly surface behaviour, in contrast to the bout-organized dives typical of longer excursions (Mori et al. 2001). Therefore, maternal attendance and foraging trip durations were obtained from TDR records.

Dives were defined as departures from the surface to depths ≥ 4 m plus the ensuing return to surface. Dives to lower depths were not considered, as they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the instrument (Beck et al. 2000). Each dive was divided into descent, bottom, and ascent phases, where: (1) descent started at the surface and ended when no further increases in depth were detected; (2) ascent was defined from the end of the dive and, with the reversed time series, ending when no further increases in depth were detected; and (3) the bottom was the period between descent and ascent phases. Dives were subsequently described by duration, maximal depth, and post-dive duration. The duration of each phase of the dive, the vertical distance covered during descent and ascent, and the cumulative vertical displacements ("wiggles") during the bottom phase also were computed by the program. These basic dive descriptors were used to estimate descent and ascent rates as $r = \delta x/\delta t$, where r is the rate (m/s), δx is vertical distance, and δt is the duration of the corresponding phase.

Dive rate was used as an index of diving effort, calculated as the sum of ascent and descent distances, plus the vertical distance covered during the bottom phase, divided by total night time spent at sea. The index has been used previously to estimate vertical distance travelled per unit time (Costa and Gales 2000). For comparison with previous studies, a second index of diving effort was calculated as the total time spent diving, divided by the total night time spent at sea. Total night time at sea was calculated following algorithms available from the National Oceanic & Atmospheric Administration (NOAA) at `http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html`.

2.2.3 Diet

Scat samples, weighing an average of 50 g, were collected at each species' colony during January and February 2002 (2001 breeding season). Although species were spatially segregated on land, seals of both species occasionally used the periphery of the colony to commute between land and sea. Therefore, samples were collected only within core areas used by lactating females and pups of each species. Samples were frozen at $-20°$ C, until laboratory analysis.

In the laboratory, scat samples were thawed overnight in warm water, and washed through 1 and 0.5 mm diameter mesh sieves. Remains of fish (otoliths, scales and bones), cephalopod (beaks), mollusc (shells), bird (feathers), and invertebrates were sorted under a dissecting microscope and stored in 70% alcohol until identification. Remains were identified to the species level where possible, using available guides

(Clarke 1986, Williams and McEldowney 1990, Smale et al. 1995) and our own reference collection at CEBC, Chizé, France. Standard length of the most frequent prey for each fur seal species was estimated using available regression equations (Williams and McEldowney 1990) of fish length against measured otolith standard length (to the nearest mm). Diet was quantified by calculating the relative numerical abundance of each prey taxon (number of individuals found relative to the total number of individuals), and frequency of occurrence of each taxon (number of samples containing the item divided by the total number of samples).

2.2.4 Statistical analyses

Dives from the same seal were not independent of one another. Furthermore, the number of foraging trips, and hence the number of dives per individual were not the same. To give each seal the same statistical weights in analyses, and to avoid pseudoreplication, the mean of each dive variable was calculated per individual during initial foraging-trip scale analyses, to allow comparison with other studies (Hurlbert 1984). The mean also was used to represent data from each individual and each hour of the day, for studying diel variation in foraging behaviour.

Variability in dive depth was used as a measure of how closely AFS and SFS followed the vertical movements of prey, if they consumed the same prey species, or else as a measure of variability in prey vertical movements. To test for differences in this variability, the coefficient of variation (CV) was calculated for each individual, and a one-way Analysis of Variance was used to test whether it differed between species.

Results are presented as means ± SE, unless noted otherwise. The Shapiro-Wilks statistic and Fligner-Killeen test were used to evaluate assumptions of normality of data distributions and homogeneity of variances, respectively, prior to analyses of variance. Effects of foraging-trip duration, species, and their interaction, on each dive variable were tested using linear mixed-effects models (Pinheiro and Bates 2000). Dietary differences were tested using two-sample Wilcoxon tests. All analyses were carried out in the GNU R system (R development Core Team 2007).

2.3 Results

We obtained data for > 250 foraging trips from > 90 females, split roughly equally between the species (AFS, $n = 49$; SFS, $n = 47$; 1-11 per female Table 2.1). Data from two SFS females deployed in winter 2003 (June 11th - July 15th) to determine their foraging behaviour during late lactation, were analyzed but excluded from interspecific comparisons, as no additional SFS females could be instrumented then.

2.3.1 Maternal attendance and foraging-trip duration

Most seals departed the colony to forage at sea between 17:00 and 20:00 local time, although departures during all afternoon were observed for AFS (Figure 2.1). Arrival times were more variable, but occurred mostly during the morning for both species. AFS females departed from the colony significantly earlier in the late afternoon (Kruskal-Wallis $\chi^2 = 27.56$, $P < 0.001$), and returned to it later in the morning ($\chi^2 = 26.48$, $P < 0.001$). Median departure and arrival times were 17:30 and 09:31 for AFS, and 18:39 and 06:44 for SFS, respectively.

A subsample of 70 seals for which complete foraging cycles (i.e. foraging trip and the subsequent maternal attendance) were documented, showed that AFS spent significantly more time at sea ($F_{1,68} = 7.69$, $P = 0.007$, arcsine transformed data) and a larger proportion of their foraging cycle at sea than SFS (AFS: $77.5\% \pm 0.30$, $n = 36$; SFS: $66.2\% \pm 0.54$, $n = 34$). The proportion of time at sea did not vary significantly throughout the breeding season ($P > 0.1$ for both AFS and SFS).

Foraging trips lasted from 0.3 to 32 d, but with a highly skewed right distribution, and an absence of trips of durations 1.00 - 1.25 d (Figure 2.2). Furthermore, 43% of all trips lasted < 1 d, so a distinction between foraging trips lasting < 1 d and > 1 d was necessary. Brief, overnight foraging trips (OFTs) were significantly more frequent for SFS (48% vs 28% for AFS, Pearson's $\chi^2 = 5.15$, $P = 0.02$, Table 2.2).

Although an analysis of inter-annual variation was not the focus of this study, a comparison of durations of long foraging trip (LFT) between years did not differ significantly for either species (Kruskal-Wallis test, $P > 0.1$). Therefore, inter-annual variation in foraging and maternal attendance behaviour was not considered in subsequent analyses.

OFTs were not limited to any particular period of the breeding season, as seals alternated irregularly between OFTs and LFTs throughout that period (Figure 2.3, upper). OFTs averaged approximately half a day in duration and did not differ significantly between species (Table 2.2). However, LFTs were about 50% significantly longer in SFS females (Table 2.2). LFTs increased significantly in duration over the breeding season (slope $= 0.92\ h \cdot d^{-1}$, $P < 0.05$), although variation was large ($r^2 = 0.29$); rate of increase was similar between species (ANCOVA $F_{1,81} = 2.67$, $P = 0.11$, Figure 2.3). Data from two SFS individual females in winter included one foraging trip each, with a duration of 30.2 and 31.9 d, respectively, much greater than values recorded during the summer.

Maternal attendances were significantly longer in SFS, following either OFTs or LFTs (Table 2.2). Concomitant with these differences, female seals stayed ashore longer after LFTs than after OFTs ($F_{1,93} = 10.2$, $P = 0.002$; non-significant species $\times$ trip-type interaction, $P > 0.1$).

2.3.2 Diving behaviour

Information from 133,010 dives was obtained from all seals overall, but 16,579 of those were from two individuals deployed in winter, so 116,431 were from the summer (Table 2.3). Diving was restricted almost entirely to the night in both species. While at sea at night, both species dove 34% of the available time, on average.

Overall, diving behaviour differed significantly between species, with SFS diving deeper and for longer periods (Table 2.3). However, maximal dive depths were higher for AFS. Mean rates of descent and ascent, as well as time spent at the bottom, were higher in SFS. Despite those differences, both species spent nearly the same effort when diving, as no significant differences were found in time spent diving (mean, 34%) or the rate of diving (mean, 1,053 $\mathrm{m} \cdot \mathrm{h}^{-1}$) during the night.

Seasonal changes in diving behaviour were apparent for SFS, as the two lactating females instrumented during winter showed reduced mean diving depths and durations (24.6 ± 0.38 m and 80.2 ± 5.6 s, respectively), compared to summer values. Maximal dive durations increased to 337.5 ± 8.8 s. Diving was mainly nocturnal (mean, 99.1%), as during the summer.

Diving behaviour varied significantly with type of foraging trip (OFT vs. LFT, linear mixed effects models, $P < 0.05$ all cases), and this factor did not show any significant interactions with species for any of the dive attributes studied ($P > 0.05$ all cases). However, the inclusion of this factor did not affect interspecific comparisons. During OFTs, seals dove to significantly greater depths, for longer periods ($F_{1,46} = 28.7$ and $F_{1,46} = 40.0$, $P < 0.001$ both cases). The deepest and longest dives for each seal were recorded during OFTs (Table 2.4). Similarly, mean descent and ascent ($F_{1,46} = 8.4$, $F_{1,46} = 9.9$) plus nocturnal dive rates ($F_{1,46} = 5.4$), were significantly greater during OFTs ($P < 0.05$ all cases).

Despite the trends just reported on, median dive depth was shallower ($F_{1,46} = 5.5$,

$P = 0.02$), and mean and median dive duration ($F_{1,46} = 17.0$ and $F_{1,46} = 20.7$), plus mean bottom time ($F_{1,46} = 20.5$) were briefer during OFTs ($P < 0.001$ in all cases). Mean dive depth and time spent diving at night did not vary with type of foraging trip ($P > 0.1$ all cases).

Differences in dive behaviour between foraging trip types and between species became more evident when diel patterns in dive depth and duration were considered (Figure 2.4). During OFTs, AFS females dove to mean depths of 28 m for most of the night, but increased dive depths to 61 m at dawn. In contrast, SFS females began diving at dusk to relatively shallow depths (24 m), but dive depths increased steadily to mean depths of 48 m at midnight, and decreased thereafter to mean depths of 39 m (Figure 2.4a). Nonetheless, the coefficient of variation (CV) in dive depth between dusk and dawn was similar between species during OFTs ($F_{1,52} = 0.004$, $P = 0.95$). Dive duration followed a similar pattern during these short trips, when AFS females made the longest dives at dusk and dawn. Dive durations were much less variable throughout the night among SFS females, despite relatively large changes in dive depths (Figure 2.4b).

Diel changes in dive depth differed between LFTs and OFTs (Figure 2.4). AFS females made their deepest dives at dusk and dawn (mean 44 and 65 m, respectively), but dove to relatively shallow depths (mean 28 m) for most of the night. Dive depths varied little from dusk until the end of the night in SFS (mean 37 m), and they increased to approximately 48 m at dawn (Figure 2.4a). Concomitant with these differences, the CV of nocturnal dive depths during LFTs was higher in AFS ($F_{1,96} = 17.1$, $P < 0.001$). Again, dive durations followed approximately the same pattern in AFS, with the longest dives at dusk and dawn, and the briefest dives in the middle of the night. Dive durations of SFS females were similar to, though less pronounced than, those of AFS (Figure 2.4b).

Dive rates were lowest at dusk and dawn, regardless of foraging-trip type or species. However, they showed different diel patterns between species and between foraging-trip types (Figure 2.5a). While on OFTs, dive rates varied greatly in SFS, being highest in the middle of the night and higher than those of AFS during that period. Dive rates were more homogeneous in LFTs for both species, but were again higher for SFS in the middle of the night. They showed peaks at dusk and dawn for AFS, associated with the deeper dives they performed during those hours. Changes in time spent diving per hour of night showed the same differences between foraging-trip types, although differences between species were evident only for the hours following dusk and prior to dawn in LFTs (Figure 2.5b).

SFS females instrumented in winter dove close to the surface between dusk and dawn, and at considerably lower mean depths (15-30 m) than those in summer. Winter dive durations were 50 - 110 s, with the longest dives after midnight and before dawn. Mean dive rates and time spent diving varied greatly, but were relatively constant throughout the night at 80 $\mathrm{m} \cdot \mathrm{h}^{-1}$, and 90 $\mathrm{s} \cdot \mathrm{h}^{-1}$, respectively, considerably lower than in summer.

2.3.3 Diet

A total of 82 scat samples were analyzed (41 from each fur seal species), yielding 2,354 sagittal otoliths, 143 cephalopod beaks, and 22 crustacean remains useful for identification. Species from the family Myctophidae dominated the fish component of the diet of both species (90.8% and 92.2% of total number of prey, respectively). The genus *Gymnoscopelus* was the most common representative of that family (AFS: 71.1%; SFS: 70.0%, Figure 2.6), and seven other fish species (from 7 families) were also identified, but in very low numbers ($< 1\%$). Seven species of cephalopod were also identified, but only one of them represented $> 1\%$ of all prey numbers (Figure 2.6).

AFS and SFS consumed the same prey species, but in different proportions ($\chi^2 = 213.2$ $P < 0.001$; test based on 10 species for which relative numbers were larger than 5 for both fur seal species). The difference was due to differences in the proportions of *Gymnoscopelus* species (*G. fraseri*, *G. piabilis*, *G. nicholsi*, and other unidentified species) and, to a lesser extent, *Electrona subaspera* (Günther, 1864) and the brachioteuthid cephalopod *Slosarczykovia circumantarctica* (Lipinski, 2001) (Figure 2.6). SFS consumed *G. fraseri* and *E. subaspera* in higher numerical proportions than did AFS, and *G. nicholsi* and the cephalopod *S. circumantarctica* were more common in the diet of AFS.

Based on regression analysis of otolith size (see Methods), standard length (SL) of *G. fraseri* consumed by the two fur seal species was similar (AFS, 82.8 ± 6.3 mm, $n = 12$; SFS, 81.5 ± 6.4 mm, $n = 102$; Mann-Whitney, $U = 645.0$, $P = 0.76$). *Gymnoscopelus piabilis* consumed by AFS was slightly larger (132.5 ± 9.8 mm, $n = 14$), but not signficantly so ($U = 776.5$, $P = 0.07$), than that consumed by SFS (129.7 ± 7.7 mm, $n = 85$).

2.4 Discussion

Antarctic and subantarctic fur seals are locally sympatric (syntopic) at Macquarie Island, Marion Island, and Iles Crozet, where they feed on the same species. At Macquarie Island and Iles Crozet they were shown to use similar foraging areas, dive to similar depths, and stay submerged for about the same amount of time. These similarities in foraging behaviour have been used to support the notion that prey ecology is the major determinant of the predators' foraging characteristics. However, the large difference in duration of lactation and in pup physiology (e.g. energy budgets and fat stores, as noted above) suggested to us that some interspecific differences in foraging ecology must occur. The results of the present study revealed interspecific differences in foraging behaviour which were not previously evident from foraging-trip-scale analyses.

2.4.1 Differences in maternal attendance and foraging-trip duration

Several studies have used the interval between departure from the colony and the first dive as an indication of travel time to the first foraging patch (Boyd et al. 1991, Page et al. 2005). In out study, the late afternoon departure and early morning arrival from the colony for most individuals indicated that both species travelled to foraging areas close to the colony, because seals dove almost exclusively at night, in common with other fur seals that dive predominantly at night (Gentry and Kooyman 1986*a*). Indeed, this was documented in a previous satellite-tracking study, in which both species were shown to forage 50 - 100 km from the colony (Bailleul et al. 2005).

We observed two distinctly different kinds of foraging trip in both species: brief (OFT) or long (LFT). This also has been observed in these species at Macquarie Island (Goldsworthy 1999). However, mean foraging-trip duration varies both geographically and temporally in AFS (2.5 - 13.1 d: Boyd and Croxall 1992, Green 1997, Lea et al. 2002*c*, Kirkman et al. 2003), and the LFT durations we observed in this study (mean, 3.47 d) fall near the lower end of values in that range. At Marion Island, with a similar marine environment around it as that found around Iles Crozet, LFT durations averaged considerably longer for AFS females: 6.0 to 9.4 d for AFS (Kirkman et al. 2003), suggesting they fed closer to the colony at Iles Crozet.

The LFT durations we observed for SFS (mean 5.23 d) were similar to those observed at Marion Island (Kirkman et al. 2002), but much briefer than those observed in an allopatric population at Amsterdam Island, where summer foraging trip durations averaged 11 d (Georges and Guinet 2000*b*). SFS females at Amsterdam Island forage in the Subtropical Front (Georges et al. 2000*a*), which is found much farther from the colony, and increasingly so throughout lactation, than the Polar and Subpolar Fronts around Iles Crozet (Sparrow et al. 1996), where this species finds food. Therefore, the proximity of these two oceanic fronts around Iles Crozet may account for the briefer durations of foraging-trips in this SFS population. This may also be the case for SFS at Marion Island (Kirkman et al. 2002).

A finding common to all 3 sites where AFS and SFS breed sympatrically is the longer duration of SFS maternal attendance, compared to AFS females (Goldsworthy 1999, Bester and Bartlett 1990). Increased frequency of brief foraging trips, and reduced duration of maternal attendance, both suggest higher energy transfer rates to offspring (Boyd et al. 1994, Arnould et al. 1996*a*, Boyd 1999). In the Amsterdam Island SFS population, however, pups from mothers making very brief or very long foraging trips suffered reduced growth rates, compared to those from mothers making trips 9 - 13 d in duration (Georges and Guinet 2000*b*), so OFTs may not always be the most profitable for mother and pup. Otherwise, females of both species would be expected to use OFTs as much as possible. Therefore, SFS females may have increased the proportion of OFTs at a cost of reducing energy transfer rates to their pups. This foraging strategy may be optimal for species with relatively long lactation, with offspring that must fast for long periods during when they have reduced energy requirements (Arnould et al. 2003). In contrast, lactating female AFS may be under stronger pressure to perform foraging trips > 1 d in duration, to transfer sufficient energy to sustain pup activity and growth during maternal absence. Indeed, lactating female AFS spent a greater proportion of their foraging cycle at sea.

2.4.2 Interspecific differences in diving behaviour and diet

The major aspects of diving behaviour of lactating female AFS and SFS in our study differed little from allopatric populations of those species (Boyd and Croxall 1992, Georges et al. 2000*b*, Lea et al. 2002*c*). However, AFS may have greater versatility in diving behaviour, as they also dive frequently during the light hours in some populations (McCafferty et al. 1998, Lea et al. 2002*c*); presumably this is related to variation in diet. In contrast, our study and another one carried out at Amsterdam Island, $< 1\%$ of all SFS dives occurred during light hours, and SFS diet consisted primarily of myctophid fish (Beauplet et al. 2004).

We documented diel changes in dive characteristics, which revealed some fine-scale ecological differences between AFS and SFS: (i) relatively deep and long dusk and dawn diving, with shallow, brief diving for most of the night in AFS, particularly during LFTs, (ii) dives to relatively constant depths and durations for most of the night, with a depth increase at dawn, and dive duration maxima at dusk and dawn during LFTs for SFS, and (iii) deep diving around midnight, decreasing to minima at dusk and dawn, with relatively constant dive duration for most of the night during OFTs for SFS. These patterns resulted in SFS diving deeper and for longer periods overall. The associated changes in night dive rate and time spent diving also indicated that they concentrated diving efforts at different times of the night. Thus, AFS females focused their dive effort in the hour immediately after dusk and before dawn during LFTs, and in the hours between midnight and dawn during OFTs. In comparison, SFS females progressively increased dive effort between dusk and dawn during LFTs, and concentrated most of it around midnight during OFTs.

The first feature (i) of AFS female dives, noted above, has been considered typical of fur seals closely tracking the vertical migration of their prey (Goebel et al. 1991, Croxall et al. 1985); such as myctophid fish in our study. Most myctophids are known to undergo migrations from deep (200 - 800 m) layers in the water column during the daytime, to a few tens of meters from the surface at night (Robison 2003). Therefore, the deep crepuscular dives performed by AFS in both types of foraging trip suggest they were following their prey, as they return to their deeper daytime locations.

The diel diving pattern of SFS in LFTs suggests that this species did not follow the vertical migrations of their prey closely (feature iii, as noted above). Consistent with this observation, variability in dive depth throughout the night was lower in SFS, and their dives were concentrated deeper in the water column, so foraging exhibited some vertical segregation between species during LFTs. This was not mirrored in nocturnal dive rates or time spent diving, as diel patterns in those variables were similar between species. The diving behaviour of SFS during LFTs is similar to that of benthic feeding otariids (Costa and Gales 2003, Arnould and Hindell 2001); however, both SFS and AFS are pelagic foragers (Bailleul et al. 2005), and the bottom phase of dives was characterized by numerous “wiggles”, which is not typical of benthic feeders. The overall similarity in the diets of both species suggests that they exploit the same prey resource, but in slightly different ways, as they distribute their dive effort differently over time and through the water column.

AFS and SFS females differed most strikingly in OFT diving characteristics. During OFTs, some of these differences resulted in vertical segregation of approximately 20 m around midnight. The nocturnal dive rate at dusk and dawn was very low for these trips among SFS, even lower than among AFS, hence they made very few dives at these times. Consistent with the reduction in dive effort at dawn, SFS females arrived at the colony earlier, and the later arrival of AFS females reflects their greater effort diving deeply at dawn.

The diet and diving behaviour of SFS have only been studied previously at Amsterdam Island. The myctophids consumed there differ greatly from those we identified (Beauplet et al. 2004), with none of the same species being noted. However, diving behaviour is strikingly similar between the 2 sites. Although OFTs do not occur at Amsterdam Island, LFT dives of SFS from both sites showed relatively constant depths throughout the night, and our limited data from winter also show similarities between the 2 sites. This contrasts with AFS studies showing broad differences in diving behaviour, in association with differences in diet. SFS may thus be less flexible in their diving behaviour than their southern cousins.

The vertical distribution and migration of myctophids consumed by fur seals in waters around Iles Crozet are unknown, but data from Iles Kerguelen (1400 km to the southeast) provide some indications. The 3 most important myctophids identified in Iles Crozet fur seal scats have been found in the upper 50 m layer of waters around Iles Kerguelen (Duhamel et al. 2000). *Gymnoscopelus fraseri* shows strong vertical migrations there, but is less abundant than *G. nicholsi* near the surface at that location. If the same pattern exists around Iles Crozet, it may explain the higher frequency of *G. fraseri* in SFS and of *G. nicholsi* in AFS scats. Interestingly, *G. nicholsi* from that location is richer in lipid content than *G. fraseri* (18.0 vs. 11.6 % wet mass; Lea et al. 2002*d*). Therefore, AFS may forage more efficiently by trading off the larger abundance of an energetically poorer prey deeper in the water column, for a richer prey closer to the surface. The consequences of such foraging behaviour differences between sympatric fur seals with contrasting lactation durations need to be investigated in terms of mother-offspring energetics.

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Table 2.1. Summary of data on lactating female Antarctic (AFS) and subantarctic (SFS) fur seals fitted with time-depth recorders (TDRs) on Iles Crozet, in the breeding seasons of 2001-02 and 2002-03

Species	Breeding Season	Body mass (kg)	TDR model				Foraging trips
			MK5	MK7	MK8	All	
AFS	2001	33.2 ± 0.44	5	16	16	37	102
	2002	31.6 ± 0.58	3	4	5	12	30
	Both	32.7 ± 0.36	8	20	21	49	132
SFS	2001	30.6 ± 0.55	3	17	17	37	113
	2002	30.4 ± 0.78	2	4	4	10	32
	Both	30.5 ± 0.45	5	21	21	47	145

Table 2.2. Summary of durations of overnight (OFT) and long (LFT) foraging trips, and of the ensuing period ashore, for Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet. Mean ± SE (N) are shown

Activity	Species	Duration (d)	
		OFT	LFT
At-sea	AFS	0.52 ± 0.03 (19)	3.47 ± 0.20 (49)
	SFS	0.48 ± 0.02 (35)	5.23 ± 0.51 (38)
	F-ratio	$F_{1,52} = 1.72$	$F_{1,85} = 12.4^{b}$
Ashore[a]	AFS	0.74 ± 0.17 (17)	1.18 ± 0.09 (31)
	SFS	1.17 ± 0.12 (28)	1.94 ± 0.19 (19)
	F-ratio	$F_{1,43} = 4.63^{b}$	$F_{1,48} = 16.0^{b}$

[a] Periods ashore were grouped according to duration of the preceding foraging trip

[b] $P < 0.01$ between species

Table 2.3. Overall summary of diving behaviour of Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet. Mean ± SE (N) are shown

Dive variable[a]	AFS	SFS	F-ratio
Total number of dives	59, 636	56, 795	
Night dives (% of total)	97.8 ± 0.04	98.5 ± 0.04	4.71[b]
Mean dive depth (m)	29.2 ± 0.24	39.7 ± 0.31	14.3[c]
Median dive depth (m)	23.7 ± 0.33	39.9 ± 0.39	19.8[c]
Maximum dive depth (m)	122.9 ± 0.66	99.8 ± 0.34	17.4[c]
Deepest dive (m)	193	141	
Mean dive duration (s)	78.5 ± 0.42	93.2 ± 0.46	10.6[b]
Median dive duration (s)	74.5 ± 0.57	94.5 ± 0.57	11.5[c]
Maximum dive duration (s)	219.0 ± 0.63	206.9 ± 0.58	3.77
Longest dive (s)	295	310	
Mean descent rate ($m \cdot s^{-1}$)	0.92 ± 0.003	1.07 ± 0.004	19.9[c]
Mean ascent rate ($m \cdot s^{-1}$)	1.07 ± 0.004	1.23 ± 0.005	12.6[c]
Mean bottom time (s)	31.8 ± 0.14	36.4 ± 0.19	7.1[b]
Time spent diving at night (% of night time)	34.5 ± 0.19	33.4 ± 0.17	0.29
Night dive rate ($m \cdot h^{-1}$)	988.5 ± 7.84	$1,116.6 \pm 8.97$	2.23

[a] For each individual, the mean was used to avoid pseudoreplication
[b] $P < 0.05$ between species
[c] $P < 0.001$ between species

Table 2.4. Quantitative summary of diving behaviour of Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet, during overnight (OFT) and long (LFT) foraging trips. Mean ± SE (N) are shown

Dive variable[b]	AFS	SFS
OFT		
Total number of dives	4,088	8,573
Mean dive depth (m)	29.7 ± 0.25	37.8 ± 0.35
Median dive depth (m)	24.2 ± 0.33	37.4 ± 0.46
Maximum dive depth (m)	122.0 ± 0.67	99.9 ± 0.36
Deepest dive (m)	193	141
Mean dive duration (s)	78.7 ± 0.44	88.1 ± 0.51
Median dive duration (s)	74.5 ± 0.58	88.3 ± 0.66
Maximum dive duration (s)	218.2 ± 0.65	207.2 ± 0.69
Longest dive (s)	295	310
Mean descent rate ($\text{m} \cdot \text{s}^{-1}$)	0.92 ± 0.003	1.07 ± 0.004
Mean ascent rate ($\text{m} \cdot \text{s}^{-1}$)	1.08 ± 0.004	1.23 ± 0.006
Mean bottom time (s)	31.5 ± 0.15	34.9 ± 0.22
Time spent diving at night (% of night time)	35.4 ± 0.20	33.1 ± 0.21
Night dive rate ($\text{m} \cdot \text{h}^{-1}$)	$1,008.9 \pm 8.17$	$1,105.8 \pm 10.92$
LFT		
Total number of dives	54,850	48,064
Mean dive depth (m)	29.6 ± 0.89	43.7 ± 0.48
Median dive depth (m)	29.7 ± 1.10	45.7 ± 0.57
Maximum dive depth (m)	92.1 ± 1.78	89.3 ± 0.70
Deepest dive (m)	151	134
Mean dive duration (s)	90.6 ± 1.37	103.7 ± 0.72
Median dive duration (s)	94.6 ± 1.79	108.0 ± 0.86
Maximum dive duration (s)	185.0 ± 1.40	180.2 ± 1.03
Longest dive (s)	220	255
Mean descent rate ($\text{m} \cdot \text{s}^{-1}$)	0.80 ± 0.01	1.04 ± 0.006
Mean ascent rate ($\text{m} \cdot \text{s}^{-1}$)	0.93 ± 0.02	1.22 ± 0.008
Mean bottom time (s)	39.6 ± 0.56	39.5 ± 0.38
Time spent diving at night (% of night time)	34.5 ± 0.68	33.1 ± 0.34
Night dive rate ($\text{m} \cdot \text{h}^{-1}$)	833.2 ± 24.16	$1,082.4 \pm 14.68$

[a] See text for results of statistical comparisons

[b] For each individual, the mean was used to avoid pseudoreplication

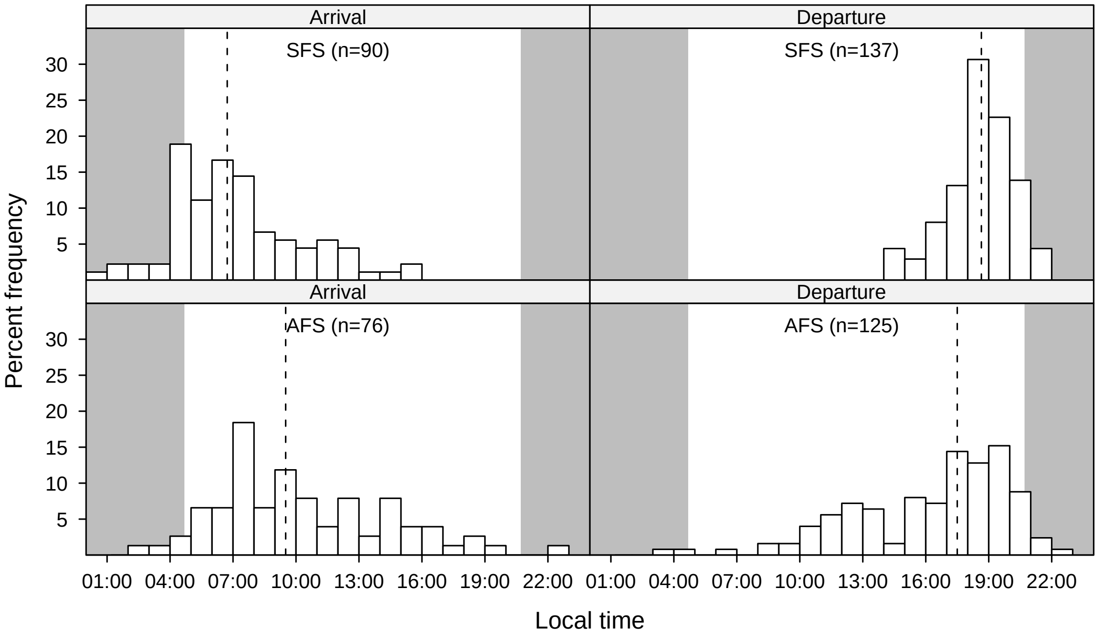

Figure 2.1. Sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet differ significantly in times of morning returns from foraging trips (left) and of afternoon departures for foraging trips (right). Shaded area: time between dusk and dawn; dashed vertical lines: median times

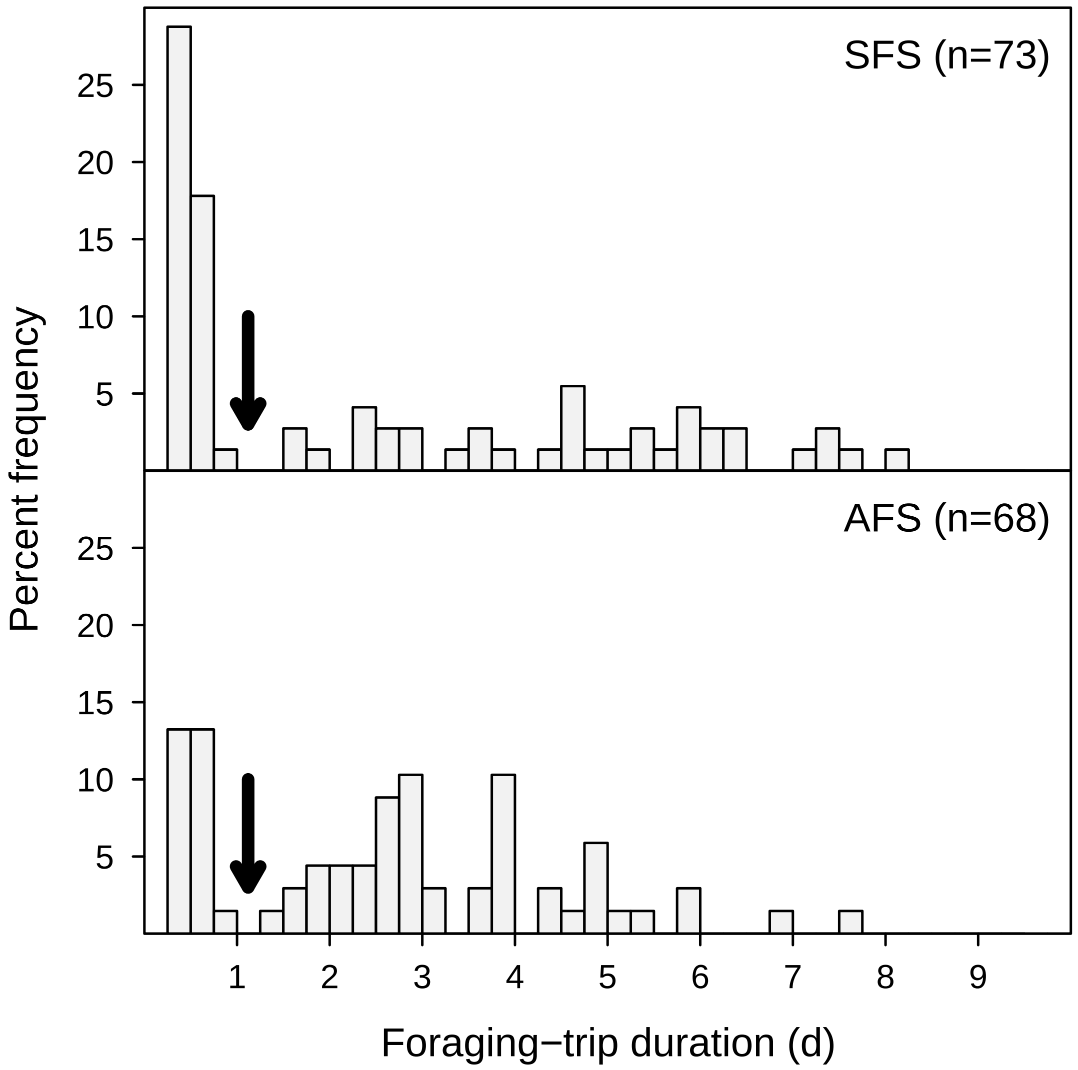

Figure 2.2. Frequency distributions of foraging-trip durations for sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet are variable and highly skewed. A discontinuity in duration is apparent (arrows), which was used to distinguish between brief and long trips (see text). Data were binned at 0.25 d

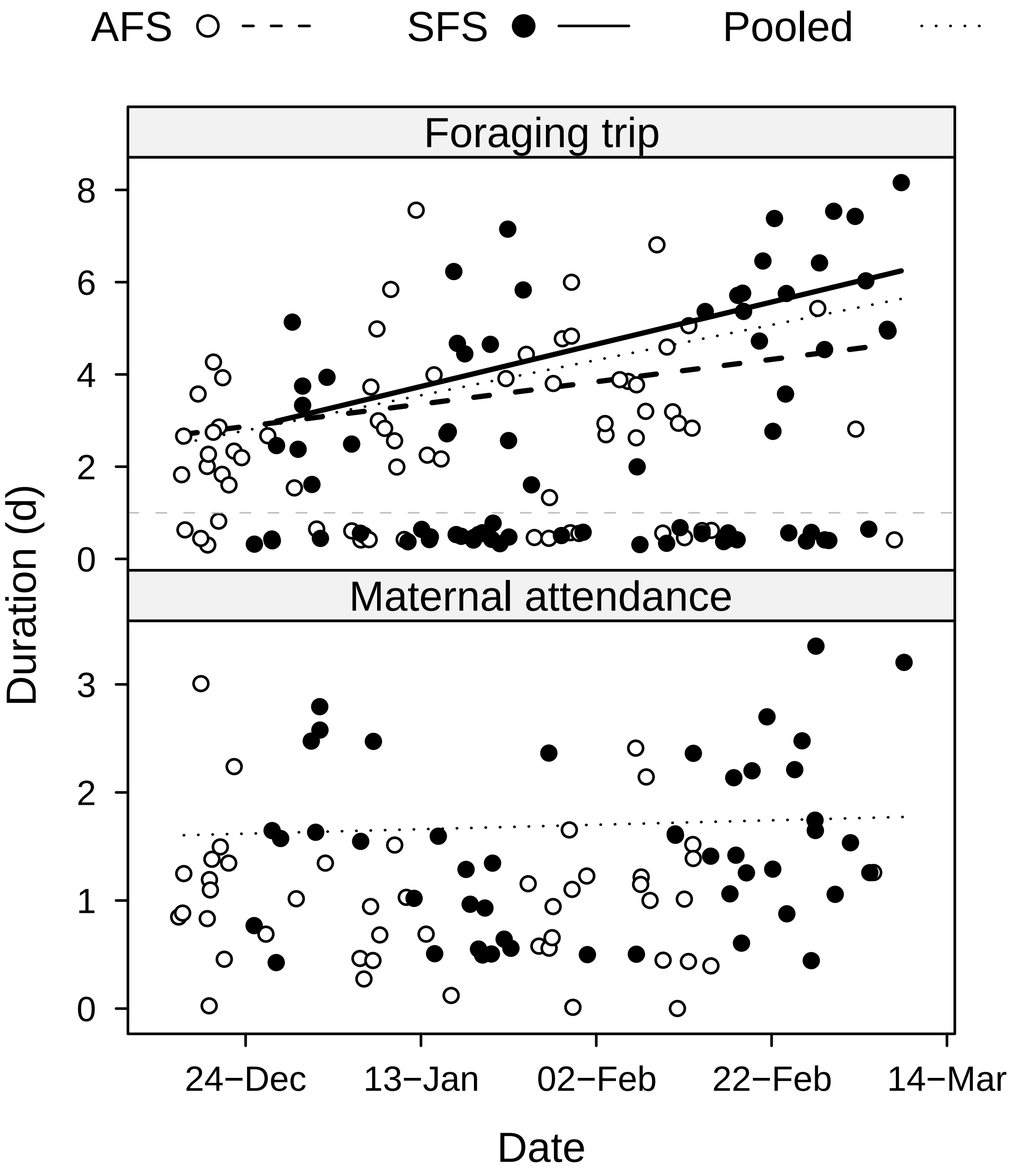

Figure 2.3. Long foraging trips (LFTs) increased in duration over the breeding season (upper) but periods of maternal attendance on land did not (lower), for sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet. Lines represent fitted linear regressions. The thin gray dashed line (upper) at 1 d separates OFTs and LFTs

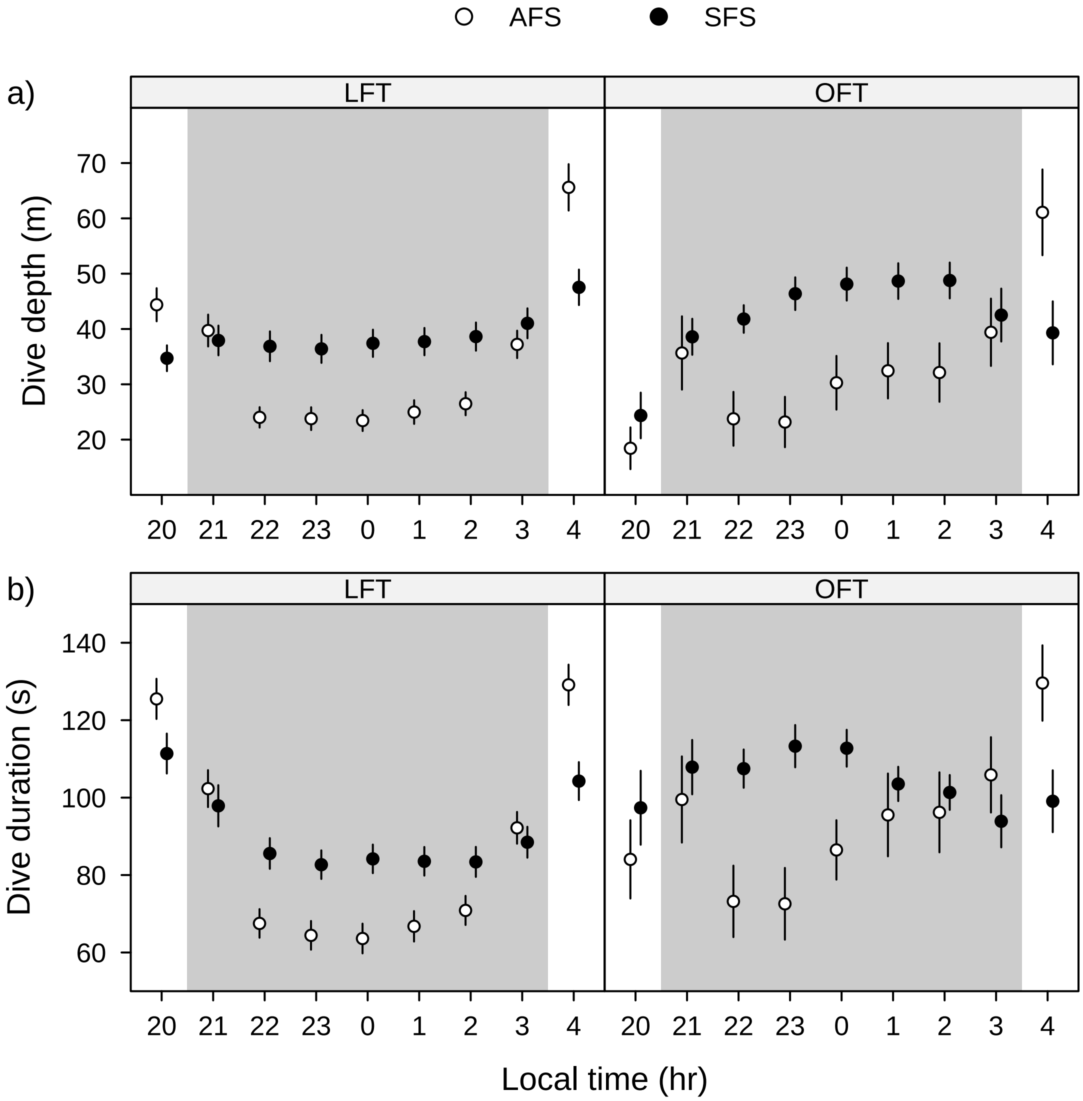

Figure 2.4. Diel patterns in depth (a) and duration (b) of foraging dives differed between sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at ILes Crozet, for overnight (OFT, right) and long (LFT, left) foraging trips. Values are mean ± SE

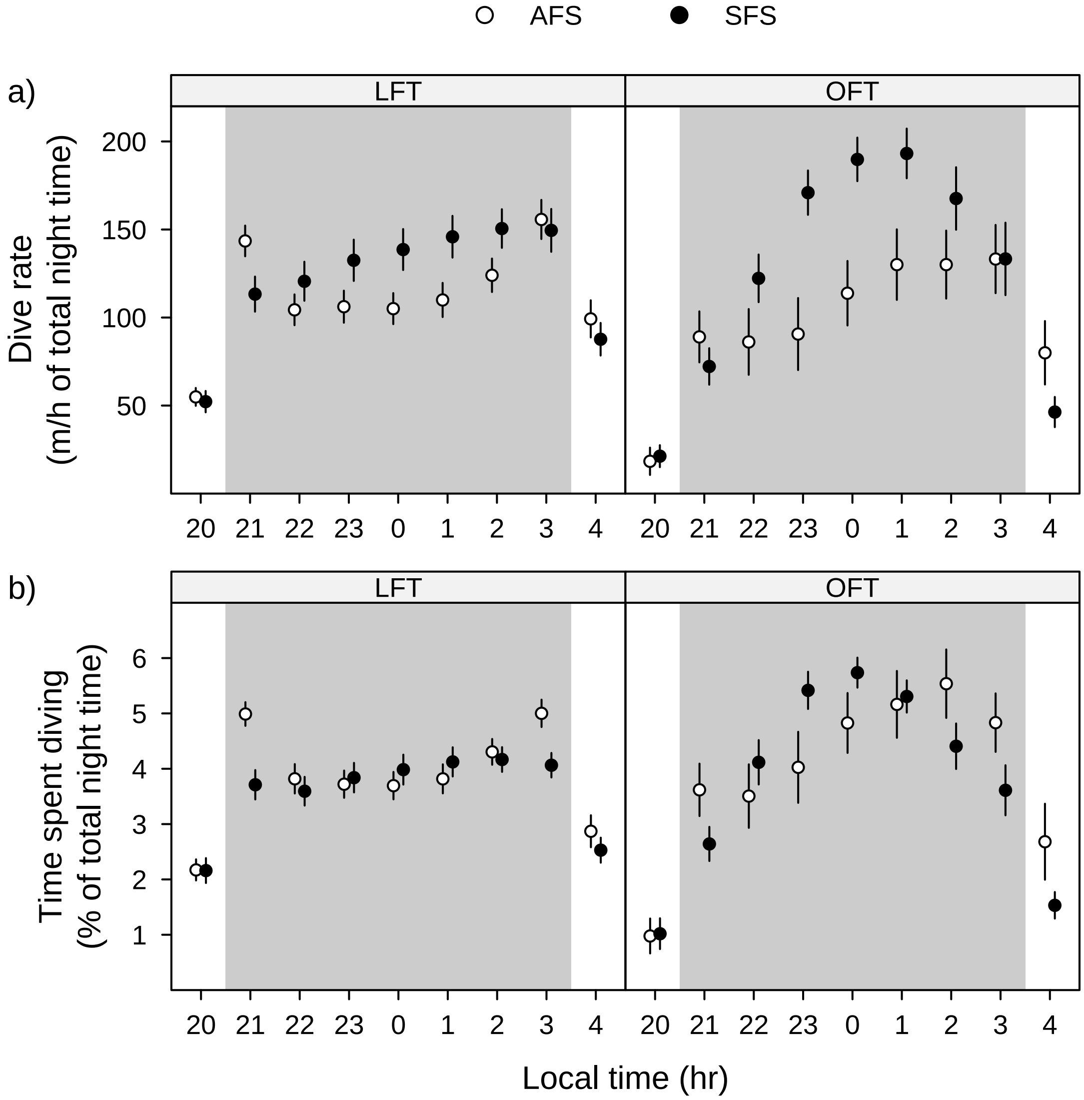

Figure 2.5. Diel patterns in nocturnal dive rate (vertical meters travelled per night hour, a), and time spent diving (b) differed between sympatric lactating Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet, for overnight (OFT, right) and long (LFT, left) foraging trips. Values are mean ± SE

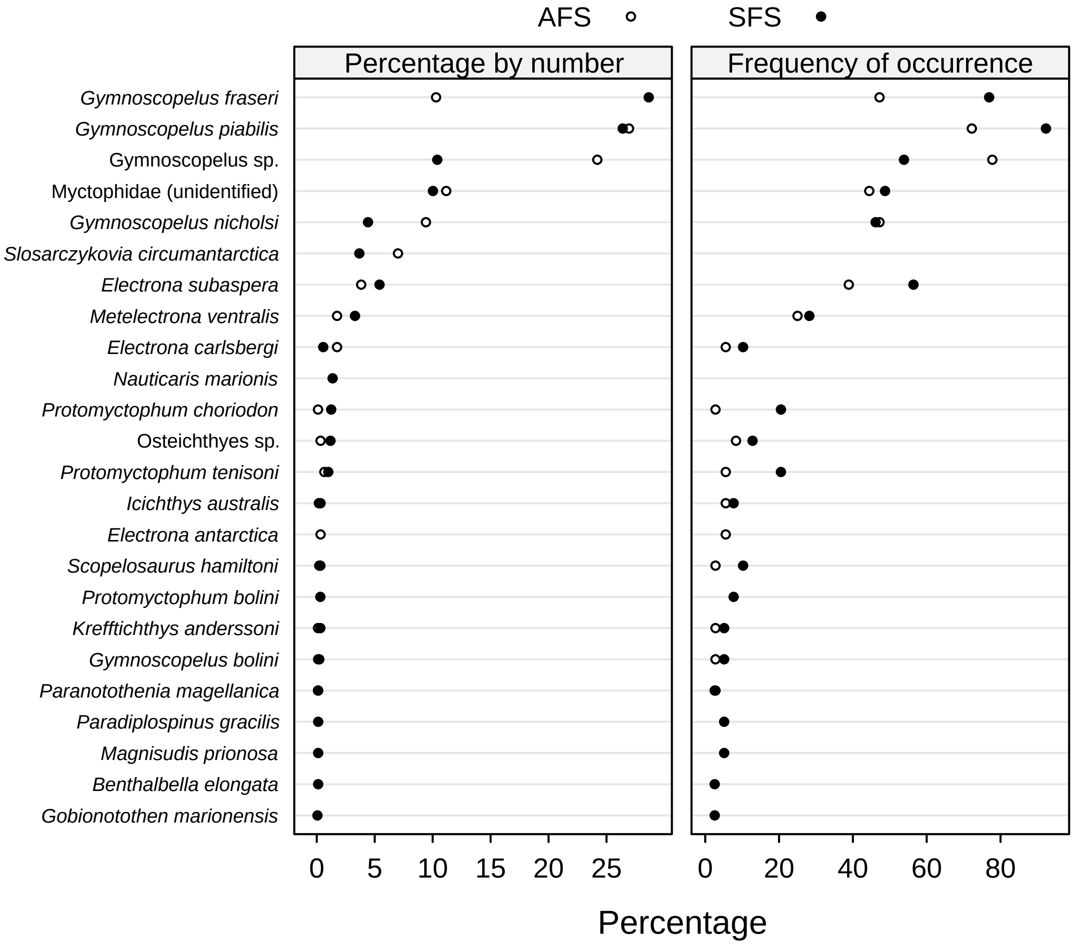

Figure 2.6. Percentage by number (of total prey items) and relative frequency of occurrence of identified prey in scat samples of Antarctic (AFS) and subantarctic (SFS) fur seals from MAE, Iles Crozet. Only those species with relative frequency or frequency of occurrence higher than 1% are shown

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RESEARCH ARTICLE

Foraging behaviour of sympatric Antarctic and subantarctic fur seals: does their contrasting duration of lactation make a difference?

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Abstract The duration of periods spent ashore versus foraging at sea, diving behaviour, and diet of lactating female Antarctic (*Arctocephalus gazella*, AFS) and subantarctic (*A. tropicalis*, SFS) fur seals were compared at Iles Crozet, where both species coexist. The large disparity in lactation duration (SFS: 10 months, AFS: 4 months), even under local sympatry, has led to the expectation that AFS should exhibit higher foraging effort or efficiency per unit time than SFS to allow them to wean their pups in a shorter period of time. Previous evidence, however, has not supported these expectations. In this study, the distribution of foraging trip durations revealed two types of trips: overnight (OFT, <1 day) and long (LFT, >1 day), in common with other results from Macquarie Island. However, diving behaviour differed significantly between foraging trip types, with greater diving effort in OFTs than in LFTs, and diving behaviour differed between fur seal species. OFTs were more frequent in SFS (48%) than in AFS (28%). SFS performed longer LFTs and maternal attendances than AFS, but spent a smaller proportion of their foraging cycle at sea (66.2 vs. 77.5%, respectively). SFS dove deeper and for longer periods than AFS, in both OFTs and LFTs, although indices of diving effort were similar between species. Diel variation in diving behaviour was lower among SFS, which foraged at greater depths during most of the night time available than AFS. The diving behaviour of AFS suggests they followed the nychthemeral migration of their prey more closely. Concomitant with the differences in diving behaviour, AFS and SFS fed on the same prey species, but in different proportions of three myctophid fish (*Gymnoscopelus fraseri*, *G. piabilis*, and *G. nicholsi*) that represented most of their diet. The estimated size of the most important fish consumed did not vary significantly between fur seal species, suggesting that the difference in dive depth was mostly a result of changes in the relative abundance of these myctophids. The energy content of these fish at Iles Crozet may thus influence the amount and quality of milk delivered to pups of each fur seal species. These results contrast with those found at other sites where both species coexist, and revealed a scale of variation in foraging behaviour which did not affect their effort while at sea, but that may be a major determinant of foraging efficiency and, consequently, maternal investment.

Introduction

Temporospatial separation of foraging and breeding is a defining characteristic of pinnipeds, and may constrain their evolution (Costa 1991). Unlike most phocid seals, otariid (fur seals and sea lions) lactating females cannot fast for the entire period of lactation, as they are too small to store all the required energy (Boness and Bowen 1996). Therefore, they alternate their time at sea foraging with visits ashore to nurse their pup. Otariid lactation varies in duration from 4 months (Antarctic *Arctocephalus gazella* and northern *Callorhinus*

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ursinus fur seals) to 3 years (Galápagos fur seals *A. galapagoensis*), and single foraging trips range from several hours to about 50 days in duration, depending on the species, stage of lactation, population, and location (Beauplet et al. 2004; Schulz 2004). Such large variation has prompted efforts to identify the proximate and ultimate factors that determine what particular strategy an otariid adopts.

Studies on temperate species have emphasized the importance of prey ecology and variability of the physical environment in relation to otariid maternal strategies. For example, Juan Fernández (*A. philippii*) and subantarctic (*A. tropicalis*) fur seals both have a 10-month lactation, during which lactating females feed on epipelagic fish (mean depths <30 m), mostly at night (Ochoa-Acuña and Francis 1995; Beauplet et al. 2004). Mean duration of foraging trips increases in both species from 1–2 days early in lactation, to 25–50 days just prior to weaning. In contrast, foraging trips of Australian fur seals (*A. pusillus doriferus*) rarely exceed 10 days during lactation, and females feed at much greater depths on benthic prey at all times of day (Gales and Pemberton 1994; Arnould and Hindell 2001). These three species inhabit temperate latitudes with similar seasonal regimes, so differences among them have challenged an early hypothesis set forth to explain the variation in fur seal foraging behaviour, that presents environmental seasonality as the main determinant of interspecific differences in foraging–nursing cycles (Gentry et al. 1986).

A drawback of interspecific comparisons using samples from different locations is that environmental variation is usually unaccounted for. However, several examples of different species breeding on the same islands exist, offering the opportunity to control for this factor. Here we compare the foraging behaviour of sympatric Antarctic (*A. gazella*) and subantarctic (*A. tropicalis*) fur seals (AFS and SFS, respectively, hereafter), two phenotypically similar sister species with large differences in duration of lactation. AFS breed mainly on islands south of the Antarctic Polar Front, while SFS do so mainly on islands just north of it, but they breed sympatrically in three groups of islands: Macquarie Island, Iles Crozet, and the Prince Edward Islands (Bonner 1999). Lactation is 116 days long in AFS (Costa et al. 1988; Lunn et al. 1993) and 300 days long in SFS (Kerley 1987; Guinet and Georges 2000), and this trait appears to be constant throughout their distribution. SFS pups were shown to have lower energy requirements and higher body fat stores, compared to AFS pups (Arnould et al. 2003), even though rate of milk consumption was only slightly higher in AFS. Therefore, AFS females have <50% of the time that SFS females have for investing in their offspring, but their offspring's energy demands may be higher (Arnould et al. 2003). Understanding how individuals of these species forage when in sympatry, yet under such different pressures, can thus help reveal which elements of foraging behaviour are species-specific and relatively invariant, and which ones are plastic and adaptively responsive to environmental influences.

The foraging ecology of AFS and SFS has been studied at various locations throughout their range, over several time scales. The diet of AFS varies geographically, with Antarctic krill (*Euphausia superba*) being the main food resource in the southern Atlantic Ocean (South Georgia, Doidge and Croxall 1985; Reid and Arnould 1996; Bouvetøya, Kirkman et al. 2000), although fish complements their diet along the Antarctic peninsula (Casaux et al. 2003) and South Shetland Islands (Daneri 1996). In the southern Indian Ocean, fish is the main prey (Marion Island, Klages and Bester 1998; Iles Kerguelen, Lea et al. 2002a; Heard Island, Green et al. 1997). Based on scat analyses, SFS at Marion Island feed predominantly on myctophid fish (Klages and Bester 1998), although stomach content analyses suggest that at Marion (Ferreira and Bester 1999) and Gough (Bester and Laycock 1985) islands they feed mostly on cephalopods and on myctophid fish at Amsterdam Island (Beauplet et al. 2004). Some studies suggest that such intraspecific dietary differences are related to the analytical techniques used, but are also associated with differences in dive behaviour, both in terms of depth and diel activity patterns (AFS at South Georgia, Croxall et al. 1985; Boyd and Croxall 1992; AFS at Iles Kerguelen, Lea et al. 2002b; SFS at Amsterdam Island, Georges et al. 2000b).

If foraging behaviour is mainly determined by prey ecology, then dietarily similar sympatric fur seal species would be expected to differ little in foraging behaviour. At the level of entire foraging trips, this expectation has been supported in studies of AFS and SFS at Macquarie Island (Goldsworthy et al. 1997; Goldsworthy 1999; Robinson et al. 2002) and Iles Crozet (Bailleul et al. 2005). The species were similar in diet at Macquarie Island and exhibited similar foraging behaviour at both sites, with females diving close to the surface, mostly at night. Summer foraging areas of the species also overlapped considerably. Other data from Marion (Bester and Bartlett 1990; Kirkman et al. 2002, 2003) and Macquarie islands (Goldsworthy 1999; Robinson et al. 2002) suggest there are no interspecific differences in the duration of foraging trips, except at Iles Crozet, where AFS made longer trips (Bailleul et al. 2005).

To date, comparisons of foraging behaviour of AFS and SFS have used the scale of the foraging trip (Bester and Bartlett 1990; Robinson et al. 2002; Kirkman et al. 2003; Bailleul et al. 2005). However, such a scale may not reveal ecologically important interspecific differences on finer scales. Night diving by fur seals is linked to the diel vertical migration of their prey (Croxall et al. 1985; Gentry 1998; Wells et al. 1999), so foraging behaviour optima are expected to show a diel pattern, particularly during the night (Mori 1998). Therefore, important interspecific differences in the temporal distribution of dive effort and depth utilization may exist. Determining when and where the species concentrate their foraging effort in the water column, in relation to the prey they exploit, may reveal patterns that are related to their different lactation strategies. Moreover, the presence of overnight and longer foraging trips in both species at some locations raises the question of whether their functions differ. These questions have not been addressed, so the objectives of this study were to compare: (1) maternal attendance and foraging trip durations; (2) diel patterns in diving, and how they vary between overnight and longer foraging trips; and (3) diet of sympatric AFS and SFS at Iles Crozet. Because of their briefer lactation and the physiological differences between AFS and SFS pups outlined above, AFS females were expected to show briefer maternal attendance periods and foraging-trip durations. For the same reasons, they also were expected to spend greater effort while diving.

Materials and methods

Fur seal study colonies

Research was carried out at La Mare Aux Elephants (MAE; 46° 22′29′′ S, 51° 40′13′′ E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001–2002 (December 4th–March 25th) and 2002–2003 (December 1st–March 16th) breeding seasons (2001 and 2002 hereafter). MAE consists of two adjacent AFS and SFS colonies, which are on different types of substrate. AFS used the northern part of the beach, composed of small- to medium-sized pebbles, with gentle slopes behind; while SFS used the southern part of the beach, composed of large boulders eroded from the steep hinterlands. Both species gave birth close to shore, but the AFS colony grew in size as the season progressed, while the other species tended to remain close to shore during the same period.

A total of 277 (AFS: 153, SFS: 124) pups were individually marked as previously described (Georges and Guinet 2000a; Arnould et al. 2003; Bailleul et al. 2005). Pup production and mean date of pupping were estimated using total pup counts (both years; including dead and living pups) on a weekly basis until no more births were observed. Peak pupping dates were 5 and 15 December (164 and 167 pups in 2001 and 2002, respectively) for AFS, and 25 and 30 December (80 and 91 pups in 2001 and 2002, respectively) for SFS. Therefore, there were inter-annual differences of up to 10 days, which suggests large environmental differences between study years (Lunn and Boyd 1993). However, Lunn and Boyd (1993) suggested that variation in pupping date at Bird Island, South Georgia, may reflect differences in environmental conditions during late gestation, rather than postpartum, which is our study period, so inter-annual differences in foraging behaviour were not fully analysed. Populations of both species have been increasing at an annual rate of about 18%, at least until 1994 (Guinet et al. 1994).

Instrumentation, maternal attendance and diving behaviour

Animal capture and handling procedures were described in Bailleul et al. (2005) Briefly, lactating females of each species were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different time-depth recorder (TDR) models was glued to the dorsal fur between the scapulae, using a two-component glue (AW 2101 Ciba Specialty Chemicals): MK5, MK7, and MK8 (Wildlife Computers, Redmond, Washington, USA). There were no significant differences in foraging trip duration, dive depth, nor dive duration between animals instrumented with different TDR models ($P > 0.5$ in all cases), so data from the three models were pooled for interspecific comparison purposes. TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. The characteristics and composition of sampled females are summarized in Table 1. Instruments were left on the seals for 1–11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals' return to the colony.

TDR data were downloaded to a portable computer on the same day the instrument was recovered, to allow redeployment of TDRs on different individuals. Visualization and analyses of the resulting regular time series of dive data were performed using custom written software, available as GNU R (R development Core Team 2006) package diveMove (Luque 2007). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e. continuous depth readings) was recorded for at least 6 h. This limit was imposed to

Table 1 Summary of data on lactating female Antarctic (AFS) and subantarctic (SFS) fur seals fitted with time-depth recorders (TDRs) on Iles Crozet, in the breeding seasons of 2001–2002 and 2002–2003

Species	Breeding season	Body mass (kg)	TDR model				Foraging trips
			MK5	MK7	MK8	All	
AFS	2001	33.2 ± 0.44	5	16	16	37	102
	2002	31.6 ± 0.58	3	4	5	12	30
	Both	32.7 ± 0.36	8	20	21	49	132
SFS	2001	30.6 ± 0.55	3	17	17	37	113
	2002	30.4 ± 0.78	2	4	4	10	32
	Both	30.5 ± 0.45	5	21	21	47	145

exclude short excursions to sea, for activities other than foraging because they contained isolated shallow dives and mainly surface behaviour, in contrast to the bout-organized dives typical of longer excursions (Mori et al. 2001). Therefore, maternal attendance and foraging trip durations were obtained from TDR records.

Dives were defined as departures from the surface to depths $\geq$4 m plus the ensuing return to the surface. Dives to lower depths were not considered because they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the instrument (Beck et al. 2000). Each dive was divided into descent, bottom, and ascent phases, where: (1) descent started at the surface and ended when no further increases in depth were detected; (2) ascent was defined from the end of the dive and, with the reversed time series, ending when no further increases in depth were detected; and (3) the bottom was the period between descent and ascent phases. Dives were subsequently described by duration, maximal depth, and post-dive duration. The duration of each phase of the dive, the vertical distance covered during descent and ascent, and the cumulative vertical displacements ("wiggles") during the bottom phase also were computed by the program. These basic dive descriptors were used to estimate descent and ascent rates as $r = \delta x/\delta t$, where r is the rate (m/s), δx is vertical distance, and δt is the duration of the corresponding phase.

Dive rate was used as an index of diving effort, calculated as the sum of ascent and descent distances, plus the vertical distance covered during the bottom phase, divided by total night time spent at sea. The index has been used previously to estimate vertical distance travelled per unit time (Costa and Gales 2000). For comparison with previous studies, a second index of diving effort was calculated as the total time spent diving, divided by the total night time spent at sea. Total night time at sea was calculated following algorithms available from the National Oceanic and Atmospheric Administration (NOAA) at http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html..

Diet

Scat samples, weighing an average of 50 g, were collected at each species' colony during January and February 2002 (2001 breeding season). Although species were spatially segregated on land, seals of both species occasionally used the periphery of the colony to commute between land and sea. Therefore, samples were collected only within core areas used by lactating females and pups of each species. Samples were frozen at −20°C, until laboratory analysis.

In the laboratory, scat samples were thawed overnight in warm water, and washed through 1 and 0.5 mm diameter mesh sieves. Remains of fish (otoliths, scales and bones), cephalopod (beaks), mollusc (shells), bird (feathers), and invertebrates were sorted under a dissecting microscope and stored in 70% alcohol until identification. Remains were identified to the species level where possible, using available guides (Clarke 1986; Williams and McEldowney 1990; Smale et al. 1995) and our own reference collection at CEBC, Chizé, France. Standard length of the most frequent prey for each fur seal species was estimated using available regression equations (Williams and McEldowney 1990) of fish length against measured otolith standard length (to the nearest mm). Diet was quantified by calculating the relative numerical abundance of each prey taxon (number of individuals found relative to the total number of individuals), and frequency of occurrence of each taxon (number of samples containing the item divided by the total number of samples).

Statistical analyses

Dives from the same seal were not independent of one another. Furthermore, the number of foraging trips, and hence the number of dives per individual were not the same. To give each seal the same statistical weights in analyses, and to avoid pseudoreplication, the mean of each dive variable was calculated per individual during initial foraging-trip scale analyses, thus allowing comparison with other studies (Hurlbert 1984). The mean also was used to represent data from each individual and each hour of the day, for studying diel variation in foraging behaviour.

Variability in dive depth was used as a measure of how closely AFS and SFS followed the vertical movements of prey, if they consumed the same prey species, or else as a measure of variability in prey vertical movements. To test for differences in this variability, the coefficient of variation (CV) was calculated for each individual, and a one-way Analysis of Variance was used to test whether it differed between species.

Results are presented as means ± SE, unless noted otherwise. The Shapiro–Wilks statistic and Fligner–Killeen test were used to evaluate assumptions of normality of data distributions and homogeneity of variances, respectively, prior to analyses of variance. Effects of foraging-trip duration, species, and their interaction, on each dive variable were tested using linear mixed-effects models (Pinheiro and Bates 2000). Dietary differences were tested using two-sample Wilcoxon tests. All analyses were carried out in the GNU R system (R development Core Team 2006).

Results

We obtained data for >250 foraging trips from >90 females, split roughly equally between the species (AFS, $n = 49$;

SFS, $n = 47$; 1–11 per female Table 1). Data from two SFS females deployed in winter 2003 (June 11th–July 15th) to determine their foraging behaviour during late lactation, were analysed but excluded from interspecific comparisons, because no additional SFS females could be instrumented then.

Maternal attendance and foraging-trip duration

Most seals departed the colony to forage at sea between 17:00 and 20:00 local time, although departures during all afternoon were observed for AFS (Fig. 1). Arrival times were more variable, but occurred mostly during the morning for both species. AFS females departed from the colony significantly earlier in the afternoon (Kruskal–Wallis $\chi^2 = 27.56$, $P < 0.001$), and returned to it later in the morning ($\chi^2 = 26.48$, $P < 0.001$). Median departure and arrival times were 17:30 and 09:31 for AFS, and 18:39 and 06:44 for SFS, respectively.

A subsample of 70 seals for which complete foraging cycles (i.e. foraging trip and the subsequent maternal attendance) were documented, showed that AFS spent significantly more time at sea ($F_{1,\,68} = 7.69$, $P = 0.007$, arcsine transformed data) and a larger proportion of their foraging cycle at sea than SFS (AFS: 77.5% ± 0.30, $n = 36$; SFS: 66.2% ± 0.54, $n = 34$). The proportion of time at sea did not vary significantly throughout the breeding season ($P > 0.1$ for both AFS and SFS).

Foraging trips lasted from 0.3 to 32 days, but with a highly skewed right distribution, and an absence of trips of durations 1.00–1.25 days (Fig. 2). Furthermore, 43% of all trips lasted <1 day, so a distinction between foraging trips lasting <1 day and >1 day was necessary. Brief, overnight foraging trips (OFT) were significantly more frequent for SFS (48 vs. 28% for AFS, Pearson's $\chi^2 = 5.15$, $P = 0.02$, Table 2).

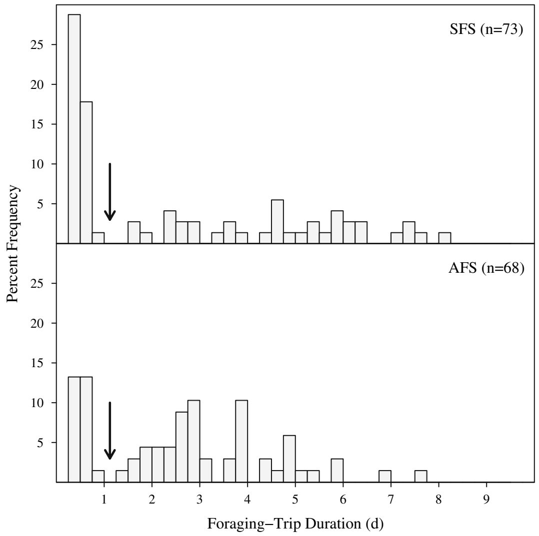

Fig. 2 Frequency distributions of foraging-trip durations for sympatric lactating female Antarctic (*AFS*) and subantarctic (*SFS*) fur seals at Iles Crozet are variable and highly skewed. A discontinuity in duration is apparent (*arrows*), which was used to distinguish between brief and long trips (see text). Data were binned at 0.25 days

Although an analysis of inter-annual variation was not the focus of this study, a comparison of durations of long foraging trips (LFT) between years did not differ significantly for either species (Kruskal–Wallis test, $P > 0.1$). Therefore, inter-annual variation in foraging and maternal attendance behaviour was not considered in subsequent analyses.

OFTs were not limited to any particular period of the breeding season because seals alternated irregularly between OFTs and LFTs throughout that period (Fig. 3, upper). OFTs averaged approximately half a day in duration and did not differ significantly between species (Table 2). However, LFTs were about 50% significantly longer in SFS females (Table 2). LFTs increased significantly in duration over the breeding season (slope = $0.92\ h \times d^{-1}$, $P < 0.05$),

Fig. 1 Sympatric lactating female Antarctic (*AFS*) and subantarctic (*SFS*) fur seals at Iles Crozet differ significantly in times of morning returns from foraging trips (*left*) and of afternoon departures for foraging trips (*right*). *Shaded area* time between dusk and dawn; *dashed vertical lines* median times

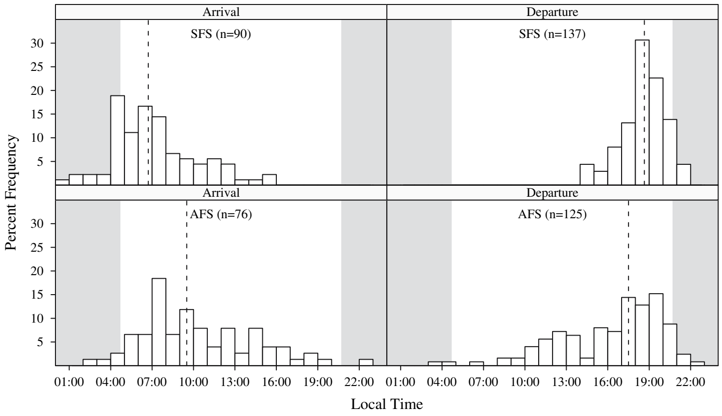

Table 2 Summary of durations of overnight (OFT) and long (LFT) foraging trips, and of the ensuing period ashore, for Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet. Mean ± SE (N) are shown

Activity	Species	Duration (d)	
		OFT	LFT
At-sea	AFS	0.52 ± 0.03 (19)	3.47 ± 0.20 (49)
	SFS	0.48 ± 0.02 (35)	5.23 ± 0.51 (38)
	F-ratio	$F_{1,52} = 1.72$	$F_{1,85} = 12.4$ [b]
Ashore[a]	AFS	0.74 ± 0.17 (17)	1.18 ± 0.09 (31)
	SFS	1.17 ± 0.12 (28)	1.94 ± 0.19 (19)
	F-ratio	$F_{1,43} = 4.63$ [b]	$F_{1,48} = 16.0$ [b]

[a] Periods ashore were grouped according to duration of the preceding foraging trip

[b] $P < 0.01$ between species

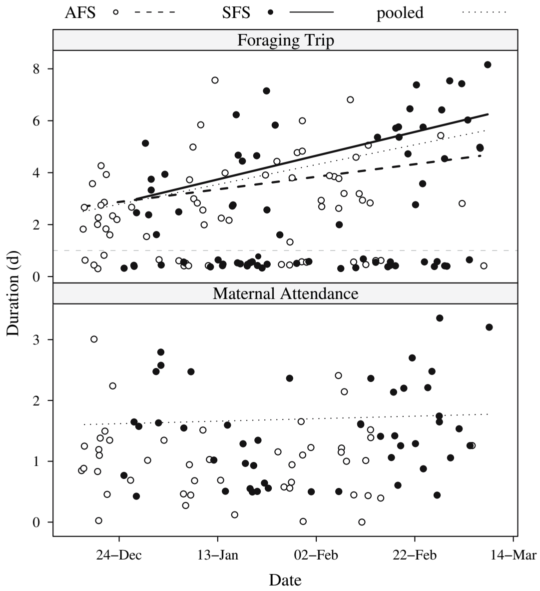

Fig. 3 Long foraging trips increased in duration over the breeding season (*upper*) but periods of maternal attendance on land did not (*lower*), for sympatric lactating female Antarctic (*AFS*) and subantarctic (SFS) fur seals at Iles Crozet. *Lines* represent fitted linear regressions. The *thin gray dashed line* (*upper*) at 1 day separates overnight and long foraging trips

Table 3 Overall summary of diving behaviour of Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet. Mean ± SE (N) are shown

Dive variable[a]	AFS	SFS	F-ratio
Total number of dives	59,636	56,795	
Night dives (% of total)	97.8 ± 0.04	98.5 ± 0.04	4.71[b]
Mean dive depth (m)	29.2 ± 0.24	39.7 ± 0.31	14.3[c]
Median dive depth (m)	23.7 ± 0.33	39.9 ± 0.39	19.8[c]
Maximum dive depth (m)	122.9 ± 0.66	99.8 ± 0.34	17.4[c]
Deepest dive (m)	193	141	
Mean dive duration (s)	78.5 ± 0.42	93.2 ± 0.46	10.6[b]
Median dive duration (s)	74.5 ± 0.57	94.5 ± 0.57	11.5[c]
Maximum dive duration (s)	219.0 ± 0.63	206.9 ± 0.58	3.77
Longest dive (s)	295	310	
Mean descent rate (m s^{-1})	0.92 ± 0.003	1.07 ± 0.004	19.9[c]
Mean ascent rate (m s^{-1})	1.07 ± 0.004	1.23 ± 0.005	12.6[c]
Mean bottom time (s)	31.8 ± 0.14	36.4 ± 0.19	7.1[b]
Time spent diving at night (% of night time)	34.5 ± 0.19	33.4 ± 0.17	0.29
Night dive rate (m h^{-1})	988.5 ± 7.84	1,116.6 ± 8.97	2.23

[a] For each individual, the mean was used to avoid pseudoreplication

[b] $P < 0.05$ between species

[c] $P < 0.001$ between species

although variation was large ($r^2 = 0.29$); rate of increase was similar between species (ANCOVA $F_{1,81} = 2.67$, $P = 0.11$, Fig. 3). Data from two SFS individual females in winter included one foraging trip each, with a duration of 30.2 and 31.9 days, respectively, much greater than values recorded during the summer.

Maternal attendances were significantly longer in SFS, following either OFTs or LFTs (Table 2). Concomitant with these differences, female seals stayed ashore longer after LFTs than after OFTs ($F_{1,93} = 10.2$, $P = 0.002$; non-significant species × trip–type interaction, $P > 0.1$).

Diving behaviour

Information from 133,010 dives was obtained from all seals overall, but 16,579 of those were from two individuals deployed in winter, so 116,431 were from the summer (Table 3). Diving was restricted almost entirely to the night in both species. While at sea at night, both species dove 34% of the available time, on average.

Overall, diving behaviour differed significantly between species, with SFS diving deeper and for longer periods (Table 3). However, maximal dive depths were higher for AFS. Mean rates of descent and ascent, as well as time spent at the bottom, were higher in SFS. Despite those differences, both species spent nearly the same effort when diving, as no significant differences were found in time spent diving (mean, 34%) or the rate of diving (mean, 1,053 m × h^{-1}) during the night.

Seasonal changes in diving behaviour were apparent for SFS, as the two lactating females instrumented during winter showed reduced mean diving depths and durations (24.6 ± 0.38 m and 80.2 ± 5.6 s, respectively), compared to summer values. Maximal dive durations increased to 337.5 ± 8.8 s. Diving was mainly nocturnal (mean, 99.1%), as during the summer.

Diving behaviour varied significantly with type of foraging trip (OFT vs. LFT, linear mixed effects models, $P < 0.05$ all cases), and this factor did not show any significant interactions with species for any of the dive attributes studied ($P > 0.05$ all cases). However, the inclusion of this factor did not affect interspecific comparisons. During OFTs, seals dove to significantly greater depths, for longer periods ($F_{1,\,46} = 28.7$ and $F_{1,\,46} = 40.0$, $P < 0.001$ both cases). The deepest and longest dives for each seal were recorded during OFTs (Table 4). Similarly, mean descent and ascent ($F_{1,\,46} = 8.4$, $F_{1,\,46} = 9.9$) plus nocturnal dive rates ($F_{1,\,46} = 5.4$), were significantly greater during OFTs ($P < 0.05$ all cases).

Table 4 Quantitative summary of diving behaviour of Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet, during overnight (OFT) and long (LFT) foraging trips. Mean ± SE (N) are shown

Dive variable[b]	AFS	SFS
OFT		
Total number of dives	4,088	8,573
Mean dive depth (m)	29.7 ± 0.25	37.8 ± 0.35
Median dive depth (m)	24.2 ± 0.33	37.4 ± 0.46
Maximum dive depth (m)	122.0 ± 0.67	99.9 ± 0.36
Deepest dive (m)	193	141
Mean dive duration (s)	78.7 ± 0.44	88.1 ± 0.51
Median dive duration (s)	74.5 ± 0.58	88.3 ± 0.66
Maximum dive duration (s)	218.2 ± 0.65	207.2 ± 0.69
Longest dive (s)	295	310
Mean descent rate (m s^{-1})	0.92 ± 0.003	1.07 ± 0.004
Mean ascent rate (m s^{-1})	1.08 ± 0.004	1.23 ± 0.006
Mean bottom time (s)	31.5 ± 0.15	34.9 ± 0.22
Time spent diving at night (% of night time)	35.4 ± 0.20	33.1 ± 0.21
Night dive rate (m h^{-1})	1,008.9 ± 8.17	1,105.8 ± 10.92
LFT		
Total number of dives	54,850	48,064
Mean dive depth (m)	29.6 ± 0.89	43.7 ± 0.48
Median dive depth (m)	29.7 ± 1.10	45.7 ± 0.57
Maximum dive depth (m)	92.1 ± 1.78	89.3 ± 0.70
Deepest dive (m)	151	134
Mean dive duration (s)	90.6 ± 1.37	103.7 ± 0.72
Median dive duration (s)	94.6 ± 1.79	108.0 ± 0.86
Maximum dive duration (s)	185.0 ± 1.40	180.2 ± 1.03
Longest dive (s)	220	255
Mean descent rate (m s^{-1})	0.80 ± 0.01	1.04 ± 0.006
Mean ascent rate (m s^{-1})	0.93 ± 0.02	1.22 ± 0.008
Mean bottom time (s)	39.6 ± 0.56	39.5 ± 0.38
Time spent diving at night (% of night time)	34.5 ± 0.68	33.1 ± 0.34
Night dive rate (m h^{-1})	833.2 ± 24.16	1,082.4 ± 14.68

[a] See text for results of statistical comparisons

[b] For each individual, the mean was used to avoid pseudoreplication

Despite the trends just reported on, median dive depth was shallower ($F_{1,\,46} = 5.5$, $P = 0.02$), and mean and median dive duration ($F_{1,\,46} = 17.0$ and $F_{1,\,46} = 20.7$), as well as mean bottom time ($F_{1,\,46} = 20.5$) were briefer during OFTs ($P < 0.001$ in all cases). Mean dive depth and time spent diving at night did not vary with type of foraging trip ($P > 0.1$ all cases).

Differences in diving behaviour between foraging trip types and between species became more evident when diel patterns in dive depth and duration were considered (Fig. 4). During OFTs, AFS females dove to mean depths of 28 m for most of the night, but increased dive depths to 61 m at dawn. In contrast, SFS females began diving at dusk to relatively shallow depths (24 m), but dive depths increased steadily to mean depths of 48 m at midnight, and decreased thereafter to mean depths of 39 m (Fig. 4a). Nonetheless, the coefficient of variation (CV) in dive depth between dusk and dawn was similar between species during OFTs ($F_{1,\,52} = 0.004$, $P = 0.95$). Dive duration followed a similar pattern during these short trips, when AFS females made the longest dives at dusk and dawn. Dive durations were much less variable throughout the night among SFS females, despite relatively large changes in dive depths (Fig. 4b).

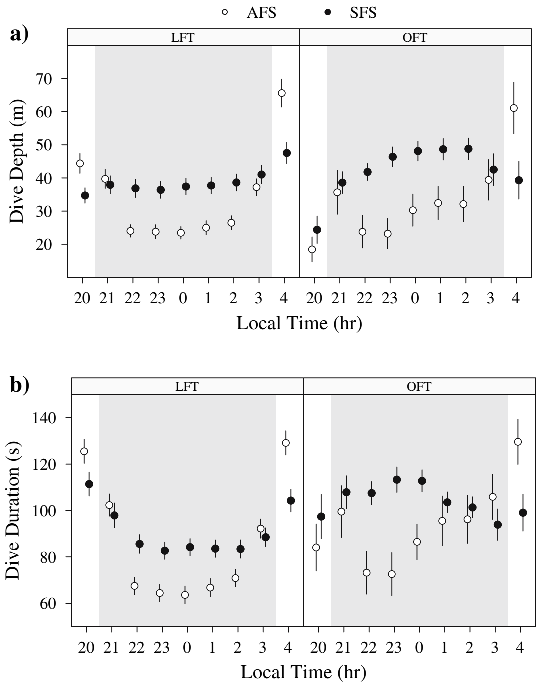

Fig. 4 Diel patterns in depth (**a**) and duration (**b**) of foraging dives differed between sympatric lactating female Antarctic (*AFS*) and subantarctic (*SFS*) fur seals at ILes Crozet, for overnight (*OFT, right*) and long (*LFT, left*) foraging trips. Values are mean ± SE

Diel changes in dive depth differed between LFTs and OFTs (Fig. 4). AFS females made their deepest dives at dusk and dawn (mean 44 and 65 m, respectively), but dove to relatively shallow depths (mean 28 m) for most of the night. Dive depths varied little from dusk until the end of the night in SFS (mean 37 m), and they increased to approximately 48 m at dawn (Fig. 4a). Concomitant with these differences, the CV of nocturnal dive depths during LFTs was higher in AFS ($F_{1,\,96} = 17.1$, $P < 0.001$). Again, dive durations followed approximately the same pattern in AFS, with the longest dives at dusk and dawn, and the briefest dives in the middle of the night. Dive durations of SFS females were similar to, though less pronounced than, those of AFS (Fig. 4b).

Dive rates were lowest at dusk and dawn, regardless of foraging-trip type or species. However, they showed different diel patterns between species and between foraging-trip types (Fig. 5a). While on OFTs, dive rates varied greatly for SFS, being highest in the middle of the night and higher than those of AFS during that period. Dive rates were more homogeneous in LFTs for both species, but were again higher for SFS in the middle of the night. They showed peaks at dusk and dawn for AFS, associated with the deeper dives they performed during those hours. Changes in time spent diving per hour of night showed the same differences between foraging-trip types, although differences between species were evident only for the hours following dusk and prior to dawn in LFTs (Fig. 5b).

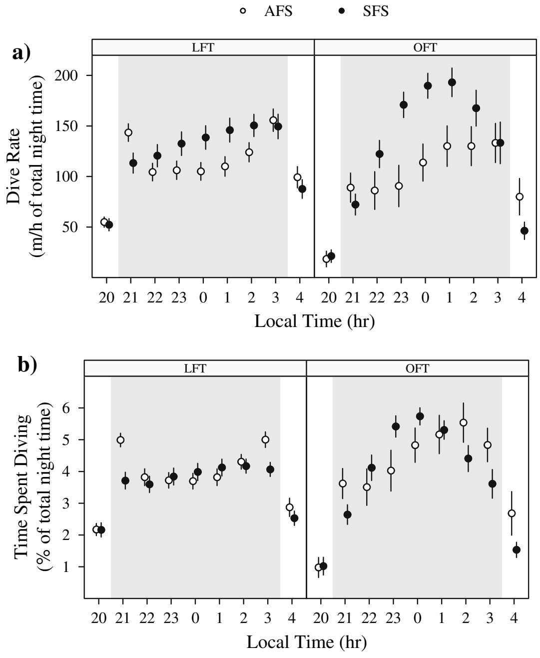

Fig. 5 Diel patterns in nocturnal dive rate (vertical meters travelled per night hour (**a**)), and time spent diving (**b**) differed between sympatric lactating Antarctic (*AFS*) and subantarctic (*SFS*) fur seals at Iles Crozet, for overnight (*OFT, right*) and long (*LFT, left*) foraging trips. Values are mean ± SE

SFS females instrumented in winter dove close to the surface between dusk and dawn, and at considerably lower mean depths (15–30 m) than those in summer. Winter dive durations were 50–110 s, with the longest dives after midnight and before dawn. Mean dive rates and time spent diving varied greatly, but were relatively constant throughout the night at 80 m × h^{-1}, and 90 s × h^{-1}, respectively; considerably lower than in summer.

Diet

A total of 82 scat samples were analysed (41 from each fur seal species), yielding 2,354 sagittal otoliths, 143 cephalopod beaks, and 22 crustacean remains useful for identification. Species from the family Myctophidae dominated the fish component of the diet of both species (90.8 and 92.2% of total number of prey, respectively). The genus *Gymnoscopelus* was the most common representative of that family (AFS: 71.1%; SFS: 70.0%, Fig. 6), and seven other fish species (from 7 families) were also identified, albeit in very low numbers (<1%). Seven species of cephalopod were also identified, but only one of them represented >1% of all prey numbers (Fig. 6).

AFS and SFS consumed the same prey species, but in different proportions ($\chi^2 = 213.2$, $P < 0.001$; test based on ten species for which relative numbers were larger than 5 for both fur seal species). The difference was due to differences in the proportions of *Gymnoscopelus* species (*G. fraseri*, *G. piabilis*, *G. nicholsi*, and other unidentified species) and, to a lesser extent, *Electrona subaspera* and the brachioteuthid cephalopod *Slosarczykovia circumantarctica* (Fig. 6). SFS consumed *G. fraseri* and *E. subaspera* in higher numerical proportions than did AFS, and *G. nicholsi* and the cephalopod *S. circumantarctica* were more common in the diet of AFS.

Based on regression analysis of otolith size (see Materials and methods), standard length of *G. fraseri* consumed by the two fur seal species was similar (AFS, 82.8 ± 6.3 mm, $n = 12$; SFS, 81.5 ± 6.4 mm, $n = 102$; Mann–Whitney, $U = 645.0$, $P = 0.76$). *G. piabilis* consumed by AFS was slightly larger (132.5 ± 9.8 mm, $n = 14$), but not significantly so ($U = 776.5$, $P = 0.07$), than that consumed by SFS (129.7 ± 7.7 mm, $n = 85$).

Discussion

Antarctic and subantarctic fur seals are locally sympatric (syntopic) at Macquarie Island, Marion Island, and Iles

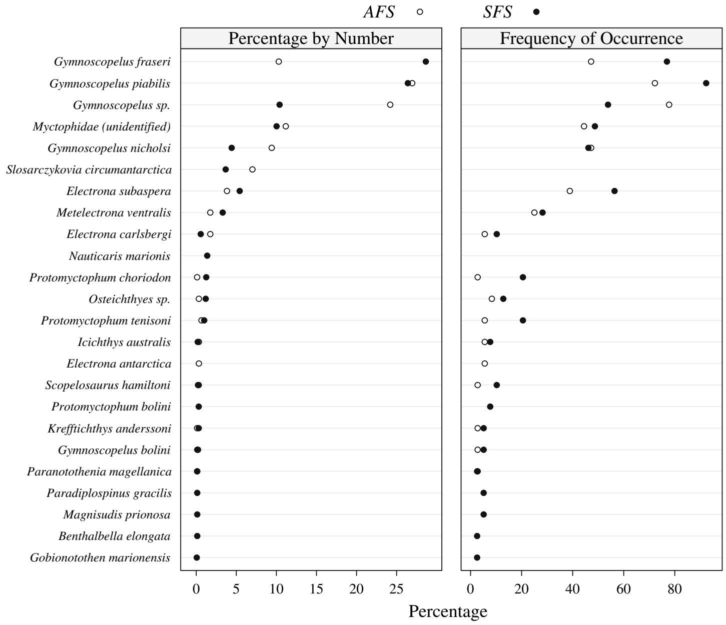

Fig. 6 Percentage by number (of total prey items) and relative frequency of occurrence of identified prey in scat samples of Antarctic (*AFS*) and subantarctic (*SFS*) fur seals from MAE, Iles Crozet. Only those species with relative frequency or frequency of occurrence higher than 1% are shown

Crozet, where they feed on the same species. At Macquarie Island and Iles Crozet they were shown to use similar foraging areas, dive to similar depths, and stay submerged for about the same amount of time. These similarities in foraging behaviour have been used to support the notion that prey ecology is the major determinant of the predators' foraging characteristics. However, the large difference in duration of lactation and in pup physiology (e.g. energy budgets and fat stores, as noted above) suggested to us that some interspecific differences in foraging ecology must occur. The results of the present study revealed interspecific differences in foraging behaviour which were not previously evident from foraging-trip scale analyses.

Differences in maternal attendance and foraging-trip duration

Several studies have used the interval between departure from the colony and the first dive as an indication of travel time to the first foraging patch (Boyd et al. 1991; Page et al. 2005). In out study, the late afternoon departure and early morning arrival from the colony for most individuals indicated that both species travelled to foraging areas close to the colony, because seals dove almost exclusively at night, in common with other fur seals that dive predominantly at night (Gentry and Kooyman 1986). Indeed, this was documented in a previous satellite-tracking study, in which both species were shown to forage 50–100 km from the colony (Bailleul et al. 2005).

We observed two distinctly different kinds of foraging trip in both species: brief (OFT) or long (LFT). This also has been observed in these species at Macquarie Island (Goldsworthy 1999). However, mean foraging-trip duration varies both geographically and temporally in AFS (2.5–13.1 days: Boyd and Croxall 1992; Green 1997; Lea et al. 2002b; Kirkman et al. 2003), and the LFT durations we observed in this study (mean, 3.47 days) fall near the lower end of values in that range. At Marion Island, which has a similar marine environment around it as that found around Iles Crozet, LFT durations averaged considerably longer for AFS females: 6.0–9.4 days (Kirkman et al. 2003), suggesting they fed closer to the colony at Iles Crozet.

The LFT durations we observed for SFS (mean 5.23 days) were similar to those observed at Marion Island (Kirkman et al. 2002), but much briefer than those observed in an allopatric population at Amsterdam Island, where summer foraging trip durations averaged 11 days (Georges and Guinet 2000b). SFS females at Amsterdam Island forage in the Subtropical Front (Georges et al. 2000a), which is found much farther from the colony, and increasingly so throughout lactation, than the Polar and Subpolar Fronts around Iles Crozet (Sparrow and Heywood 1996), where this species finds food. Therefore, the proximity of these two oceanic fronts around Iles Crozet may account for the briefer durations of foraging-trips in this SFS population. This may also be the case for SFS at Marion Island (Kirkman et al. 2002).

A finding common to all three sites where AFS and SFS breed sympatrically is the longer duration of SFS maternal attendance, compared to AFS females (Goldsworthy 1999; Bester and Bartlett 1990). Increased frequency of brief foraging trips, and reduced duration of maternal attendance, both suggest higher energy transfer rates to offspring (Boyd et al. 1994; Arnould et al. 1996; Boyd 1999). In the Amsterdam Island SFS population, however, pups from mothers making very brief or very long foraging trips suffered reduced growth rates, compared to those from mothers making trips 9–13 days in duration (Georges and Guinet 2000b), so OFTs may not always be the most profitable for mother and pup. Otherwise, females of both species would be expected to use OFTs as much as possible. Therefore, SFS females may have increased the proportion of OFTs at a cost of reducing energy transfer rates to their pups. This foraging strategy may be optimal for species with relatively long lactation, with offspring that must fast for long periods during which they have reduced energy requirements (Arnould et al. 2003). In contrast, lactating female AFS may be under stronger pressure to perform foraging trips >1 days in duration, to transfer sufficient energy to sustain pup activity and growth during maternal absence. Indeed, lactating female AFS spent a greater proportion of their foraging cycle at sea.

Interspecific differences in diving behaviour and diet

The major aspects of diving behaviour of lactating female AFS and SFS in our study differed little from allopatric populations of those species (Boyd and Croxall 1992; Georges et al. 2000b; Lea et al. 2002b). However, AFS may have greater versatility in diving behaviour, as they also dive frequently during the light hours in some populations (McCafferty et al. 1998; Lea et al. 2002b); presumably this is related to variation in diet. In contrast, our study and another one carried out at Amsterdam Island, <1% of all SFS dives occurred during light hours, and SFS diet consisted primarily of myctophid fish (Beauplet et al. 2004).

We documented diel changes in dive characteristics, which revealed some fine-scale ecological differences between AFS and SFS: (i) relatively deep and long dusk and dawn diving, with shallow, brief diving for most of the night in AFS, particularly during LFTs, (ii) dives to relatively constant depths and durations for most of the night, with a depth increase at dawn, and dive duration maxima at dusk and dawn during LFTs for SFS, and (iii) deep diving around midnight, decreasing to minima at dusk and dawn, with relatively constant dive duration for most of the night during OFTs for SFS.

These patterns resulted in SFS diving deeper and for longer periods overall. The associated changes in night dive rate and time spent diving also indicated that they concentrated diving efforts at different times of the night. Thus, AFS females focused their diving effort in the hour immediately after dusk and before dawn during LFTs, and in the hours between midnight and dawn during OFTs. In comparison, SFS females progressively increased diving effort between dusk and dawn during LFTs, and concentrated most of it around midnight during OFTs.

The first feature (i) of AFS female dives, noted above, has been considered typical of fur seals closely tracking the vertical migration of their prey (Goebel et al. 1991; Croxall et al. 1985); such as myctophid fish in our study. Most myctophids are known to undergo migrations from deep (200–800 m) layers in the water column during the daytime, to a few tens of metres from the surface at night (Robison 2003). Therefore, the deep crepuscular dives performed by AFS in both types of foraging trip suggest they were following their prey, as they return to their deeper daytime locations.

The diel diving pattern of SFS in LFTs suggests that this species did not follow the vertical migrations of their prey closely (feature ii, as noted above). Consistent with this observation, variability in dive depth throughout the night was lower in SFS, and their dives were concentrated deeper in the water column, so foraging exhibited some vertical segregation between species during LFTs. This was not mirrored in nocturnal dive rates or time spent diving, as diel patterns in those variables were similar between species. The diving behaviour of SFS during LFTs is similar to that of benthic feeding otariids (Costa and Gales 2003; Arnould and Hindell 2001); however, both SFS and AFS are pelagic foragers (Bailleul et al. 2005) and the bottom phase of dives was characterized by numerous “wiggles”, which is not typical of benthic feeders. The overall similarity in the diets of both species suggests that they exploit the same prey resource, but in slightly different ways, as they distribute their diving effort differently over time and through the water column.

AFS and SFS females differed most strikingly in OFT diving characteristics. During OFTs, some of these differences resulted in vertical segregation of approximately 20 m around midnight. The nocturnal dive rate at dusk and dawn was very low for these trips among SFS, even lower than among AFS, hence they made very few dives at these times. Consistent with the reduction in diving effort at dawn, SFS females arrived at the colony earlier, and the later arrival of AFS females reflects their greater effort diving deeply at dawn.

The diet and diving behaviour of SFS have only been studied previously at Amsterdam Island. The myctophids consumed there differ greatly from those we identified (Beauplet et al. 2004), with none of the same species being noted. However, diving behaviour is strikingly similar between the two sites. Although OFTs do not occur at Amsterdam Island, LFT dives of SFS from both sites showed relatively constant depths throughout the night, and our limited data from winter also show similarities between the two sites. This contrasts with AFS studies showing broad differences in diving behaviour, in association with differences in diet. SFS may thus be less flexible in their diving behaviour than their southern cousins.

The vertical distribution and migration of myctophids consumed by fur seals in waters around Iles Crozet are unknown, but data from Iles Kerguelen (1,400 km to the southeast) provide some indications. The three most important myctophids identified in Iles Crozet fur seal scats have been found in the upper 50 m layer of waters around Iles Kerguelen (Duhamel et al. 2000). *G. fraseri* shows strong vertical migrations there, but is less abundant than *G. nicholsi* near the surface at that location. If the same pattern exists around Iles Crozet, it may explain the higher frequency of *G. fraseri* in SFS and of *G. nicholsi* in AFS scats. Interestingly, *G. nicholsi* from that location is richer in lipid content than *G. fraseri* (18.0 vs. 11.6% wet mass; Lea et al. 2002c). Therefore, AFS may forage more efficiently by trading off the larger abundance of an energetically poorer prey deeper in the water column, for a richer prey closer to the surface. The consequences of such foraging behaviour differences between sympatric fur seals with contrasting lactation durations need to be investigated in terms of mother–offspring energetics.

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Chapter 3

Temporal structure of diving behaviour as an indicator of foraging habitat characteristics

3.1 A maximum likelihood approach for identifying dive bouts improves accuracy, precision, and objectivity

Abstract

Foraging behaviour frequently occurs in bouts, and considerable efforts to properly define those bouts have been made because they partly reflect different scales of environmental variation. Methods traditionally used to identify such bouts are diverse, include some level of subjectivity, and their accuracy and precision is rarely compared. Therefore, the applicability of a maximum likelihood estimation method (MLM) for identifying dive bouts was investigated and compared with a recently proposed sequential differences analysis (SDA). Using real data on interdive durations from Antarctic fur seals (*Arctocephalus gazella* (Peters, 1875) Peters 1875), the MLM-based model produced briefer BEC and more precise parameter estimates than the SDA approach. The MLM-based model was also in better agreement with real data, as it predicted the cumulative frequency of differences in interdive duration more accurately. Using both methods on simulated data showed that the MLM-

based approach produced less biased estimates of the given model parameters than the SDA approach. Different choices of histogram bin widths involved in SDA had a systematic effect on the estimated BEC, such that larger bin widths resulted in longer BECs. These results suggest that using the MLM-based procedure with the sequential differences in interdive durations, and possibly other dive characteristics, may be an accurate, precise, and objective tool for identifying dive bouts.

3.1.1 Introduction

Many seabirds and marine mammals dive in bouts (Gentry et al. 1986, Huin and Prince 1997, Kato et al. 2003); i.e., most of their dives occur in rapid succession, while the remaining are separated by longer intervals. Dives occurring in the same bout tend to resemble each other more than those occurring in different bouts. Based on their characteristics (e.g., mean dive depth and time spent at the bottom of the dive), bouts can be associated with a particular activity, such as travelling or foraging (Lea et al. 2002*c*). Numerous studies use dive bouts to infer instances of a forager exploiting discrete prey patches (Boyd 1996, Harcourt et al. 2002, Mori et al. 2002, Mori and Boyd 2004*a*), because food resources are patchily distributed (Wroblewski et al. 1975, Croxall et al. 1985) at scales that organisms respond to (With and Crist 1995, Wu and Loucks 1995). Depending on the scale(s) at which food resources display patchiness (Wiens 1976, Levin 1992), the same argument is applied more generally to most animal behaviours associated with foraging, in both terrestrial (e.g., Munger 1984, Schaefer and Messier 1995, Rotenberry and Wiens 1998) and aquatic environments (e.g., Kruuk et al. 1990, Fauchald 1999). Therefore, it is essential to accurately and objectively identify behavioural bouts in studies of foraging ecology of aquatic and terrestrial predators. This can be achieved by determining a bout ending criterion (BEC), or how long an interval between two successive dives should be to assign them to different bouts.

The theory and methods used to determine the BEC have been reviewed elsewhere (Slater and Lester 1982, Tolkamp and Kyriazakis 1999). Events occurring in bouts are thought to be generated by a combination of two or more processes operating on progressively larger time scales. At the smallest scale, events are separated by similar and brief intervals. Events separated by markedly longer intervals define different groups of events (or bouts), thereby distinguishing the scale at which one process generates individual events from that generating bouts. Processes of both types are thought to follow a random Poisson distribution, where the intervals between them are described by a mixture of exponential distributions (Slater and Lester 1982). Defining the BEC is, therefore, a problem of finding the time intervals that separate each process from the others.

Methods for searching the BEC include log-survivorship and log-frequency analysis (Gentry and Kooyman 1986*b*, Sibly et al. 1990). Boyd (1996) developed an iterative method to group dives into bouts by comparing the interdive duration of a given dive with the mean of those preceding it, considering it as part of a new bout if these values differed significantly. More recently, Mori et al. (2001) suggested another method, termed sequential differences analysis (SDA hereafter), based on log-frequency analysis. The BEC in this method could be estimated using the absolute differences between interdive durations, rather than the interdive durations themselves. If the occurrence of dives can be described by a mixture of Poisson distributions, the mean interdive duration should be the same for all bouts (Karlis and Xekalaki 2005). However, in cases where dive bouts are considered as instances of a diver foraging in patches, interdive duration is expected to vary between bouts because it is closely related to dive depth (Houston and Carbone 1992, Carbone and Houston 1996, Boyd 1997), which in turn depends on prey species composition and determines foraging patch quality for the predator (Thompson and Fedak 2001). Mori et al. (2001), therefore, pointed out that previous methods may erroneously assume that mean interdive duration is common to all bouts; an assumption that can be avoided with SDA.

Although SDA has been useful in studies of foraging behaviour (Mori 1998*b*, Mori and Boyd 2004*b*, Mori et al. 2005), it is based on fitting a non-linear model to the logarithm of frequencies of absolute differences in interdive durations, and possibly other dive characteristics (e.g., dive depth). SDA relies on the construction of a histogram, using the midpoints of each class as the independent variable (Sibly et al. 1990). Therefore, a certain level of subjectivity is involved in the selection of class widths, and some information is lost by summarizing data from each class with a single value. Furthermore, class widths must be adjusted, or a weighting scheme must be implemented, to avoid empty classes. There are currently no objective criteria for dealing with these factors. Johnson et al. (2006) recently pointed out that the choices made throughout this procedure can have large influences on the BEC.

Some of these issues have been raised by Langton et al. (1995), and proposed to address them by using a maximum likelihood estimation method (MLM hereafter) for defining the BEC. This approach uses the information in the entire dataset of intervals between events. Unfortunately, the method has not been adopted to identify behavioural bouts in general, and dive bouts of marine predators in particular, where understanding spatiotemporal variation in prey distribution and quality is of major interest. Our aim was, therefore, to demonstrate the usefulness of this approach in this field, incorporating the concept used in SDA to avoid the assumption of invariant mean dive characteristics between dive bouts. We used time-depth recorder (TDR) data from lactating female Antarctic fur seal (*Arctocephalus gazella* (Peters, 1875)), during their foraging trips at sea, to compare models of the frequency of differences in interdive duration fit using SDA vs. those fit using MLM.

3.1.2 Methods

Data were obtained from lactating female Antarctic fur seals at La Mare aux Elephants (MAE; 46°22’29” S, 51°40’13” E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001-02 (4 December - 25 March) and 2002-03 (1 December - 16 March) breeding seasons.

Instrumentation and measurement of diving behaviour

Animal capture and handling procedures were described in Bailleul et al. (2005). Briefly, lactating females were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different time-depth recorder (TDR) models was glued to the dorsal fur between the scapulae, using a two-component glue (AW 2101 Ciba Specialty Chemicals): MK5, MK7, and MK8 (Wildlife Computers, Redmond, Washington, U.S.A.). TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. Instruments were left on the seals for 1 to 11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals’ return to the colony.

TDR data were downloaded to a portable computer, where analyses of the resulting time series of dive data were performed using custom written software, available as `GNU R` (R development Core Team 2007) package `diveMove` (Luque 2007). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e., continuous depth readings) was available for at least 6 h. This limit was selected to exclude short excursions to sea for activities other than foraging, because these contained isolated shallow dives and mainly surface behaviour.

Dives were defined as departures from the surface to depths ≥ 4 m plus the ensuing return to surface. Dives to shallower depths were not considered because they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the instrument (Beck et al. 2000). Dives were thus described by their duration, maximal depth, and interdive duration.

For the purposes of this paper, data from the first recorded foraging trip to sea of four randomly selected individual seals were used in subsequent analyses. The models described below were fitted to each seal's dive record separately because foraging trip durations varied between them, and to avoid effects of interindividual variation in diving behaviour masking bout structure.

Identifying bouts using SDA

The variable used for defining bouts with SDA- and MLM-based methods was the absolute difference in interdive duration (t); the time between a dive and the preceding one. This procedure is based on a log-frequency analysis described in detail by Sibly et al. (1990) and further developed by Mori et al. (2001). Briefly, the first step of the method consists of creating a histogram of t, with the frequencies expressed as a logarithm. Because large values of t are considerably less frequent than small ones, some class intervals may have a frequency of zero, leading to the erroneous representation of frequencies in larger class intervals. To correct for this effect, the frequency of class intervals following intervals with zero frequency was divided by the number of preceding empty intervals plus one. The logarithm of the frequencies of all class intervals where frequency > 0 is thus considered a function of the midpoint of the intervals.

The distribution of t is assumed to be a mixture of two random Poisson processes; a fast and a slow one (Sibly et al. 1990). The fast process represents the small time scale at which individual dives occur, while the slow process represents the large time scale where bouts are distinguished. Therefore, the relationship described above can be defined as the sum of both processes:

$$y = log[N_f \lambda_f e^{-\lambda_f t} + N_s \lambda_s e^{-\lambda_s t}] \tag{3.1}$$

where y is the logarithm of the frequency of any given t; the subscripts $_f$ and $_s$ denote the fast and slow processes, respectively; N is the number of interdive intervals occurring in each process; and λ represents the probability of an event occurring in a given process per unit time (Sibly et al. 1990). Initial values for the N and λ parameters must be obtained in order to fit this negative exponential function. The broken-stick method was used for this purpose, following Sibly et al. (1990).

The BEC defining the threshold between the two Poisson processes can be obtained from eq. (3.1):

$$BEC = \frac{1}{\lambda_f - \lambda_s} log \frac{N_f \lambda_f}{N_s \lambda_s} \tag{3.2}$$

To assess the effect of the choice of histogram bin widths on the estimation procedure, the model was fit, and the BEC calculated using bin widths from 5 (i.e., the sampling resolution) to 50 s.

Identifying bouts using MLM

Langton et al. (1995) suggested that eq. (3.1) did not consider that the total number of events observed should be equal to $N_f + N_s$, and hence that the model can be simplified by expressing one of these parameters as a function of the other. The authors presented also a maximum likelihood estimation method using all observed data, rather than a histogram of these, to describe the frequency of any given event. The log likelihood of all the N_t absolute differences in interdive duration can be expressed as:

$$log\ L_2 = \sum_{i=1}^{N_t} log[p\lambda_f e^{-\lambda_f t_i} + (1-p)\lambda_s e^{-\lambda_s t_i}] \tag{3.3}$$

where p is a mixing parameter representing the proportion of fast to slow process events in the sampled population. The parameters from eq. (3.3) must be estimated numerically, hence an optimization procedure is required using appropriate initial values. These values were obtained by first maximizing a reparameterized version of eq. (3.3) using a logit transformation of the p parameter, and a logarithm transformation of the λ parameters. Initial values for this reparameterized model were in turn calculated as for the SDA (i.e., by using the broken-stick method). Such transformations stabilized the variance in the parameters, and rescaled them to avoid difficulties with the optimization algorithm. The parameter estimates obtained from this procedure were untransformed, and used as initial values for maximizing eq. (3.3). Therefore, parameter estimates and their standard errors were obtained in their original scales.

The BEC in this case was estimated analogously to eq. (3.2):

$$BEC = \frac{1}{\lambda_f - \lambda_s} log \frac{p\lambda_f}{(1-p)\lambda_s} \tag{3.4}$$

Comparison between methods

Models describing the distribution of interdive differences in dive duration (t) should accurately predict t's relative cumulative frequency. The expected relative cumulative frequency (f_c) of t can be calculated from parameters in models (3.1) and (3.3) using:

$$f_c = 1 - pe^{-\lambda_f t} - (1-p)e^{\lambda_s t} \tag{3.5}$$

Thus, f_c for the range of observed t, and the actual relative cumulative frequency distribution of t were also calculated. The observed and expected relative cumulative frequencies of t were plotted simultaneously against t (logarithmically transformed) to compare the fit of the two models to data, as proposed by Langton et al. (1995). Differences in model outcomes, relative to observed cumulative frequencies, were tested by comparing the squared residuals (observed - predicted values, squared) between the models with a paired Student's t-test (Zar 1996).

Standard errors (SEs) for each parameter estimate provided a measure of the precision of each fitted model, and hence that of the estimated BEC. Bias was compared using simulated data generated with chosen mixing (p) and probability (λ) parameters. Based on the mid-range of observed data for all four seals, the mixing parameter was set to 0.7, and values for the probability parameters were set to 0.05 and 0.005 (λ_f, and λ_s, respectively). Thus, one thousand values for t were simulated 100 times with these values, by generating a mixture of two random samples with exponential distribution ($f(\lambda_x, t) = \lambda_x e^{-\lambda_x t}$): one with $\lambda_x = 0.05$ if a random uniform variable x ($1 >= x >= 0$) from the total of 100 was < 0.7, and another with $\lambda_x = 0.005$ otherwise. Each simulated mixture was fit with both models, using the respective methods described above. The bias of the estimates in the simulations, with respect to the true value for the parameters, were subsequently calculated and compared. All data manipulations and computations were done in the GNU R statistical system and programming language (R development Core Team 2007).

To compare the effect of each method on interpretations of the behaviour of study animals, each seal's dive record was divided into bouts using the estimated BECs. The mean and variance of bout duration and interval between bouts was calculated and compared between models for each seal using Wilcoxon rank sum and Fligner-Killeen tests, respectively (Conover et al. 1981).

3.1.3 Results

The number of dives observed for each seal varied from 910 to 1,881 (Table 3.1). Probability parameter (λ) estimates from these samples were larger using MLM compared to those obtained through SDA. Conversely, the mixing parameter (p) was consistently smaller using MLM, and the total number of interdive intervals ($N_f + N_s$) was largely overestimated using SDA. As a result of these differences, estimated BECs were markedly larger using SDA, by factors ranging from 2 to 6 (Table 3.1). SEs of estimated parameters were generally smaller using MLM. More importantly, the total number of bouts identified for each seal was considerably smaller when using SDA (Table 3.1).

Varying the bin width for creating the histograms used in SDA resulted in systematic changes in most parameters: estimated BECs and numbers of interdive intervals (N_f and N_s) increased, but λ_f tended to decrease. SEs of estimated parameters increased as class bin widths were increased (Table 3.1). Using the narrowest bin width for the sampling interval programmed for TDRs (5 s), variation in estimated BECs among seals was larger using SDA than MLM (range 91.3 - 191.2 vs. 43.8 - 59.5 s).

Estimated and observed cumulative frequencies differed for high but non-asymptotic t values, regardless of the model (Figure 3.1). However, such departures were larger for models fit through SDA. Models fit through MLM followed the observed cumulative frequencies more closely, although they underestimated these frequencies for large t values (Figure 3.1). The sum of squared residuals from MLM-derived frequencies (relative to observed) ranged from 0.06 to 0.09, and from 0.5 to 1.0 for SDA-derived frequencies. The difference between models was significant for all seals

(Figure 3.1).

Bias of estimated parameters from models of simulated t values were 0.001, 0.0002, 0.00002 when fit through MLM, and 0.031, -0.0028, -0.0010 when fit through SDA (p, λ_f, λ_s, respectively). Thus, biases were smaller, and variation for each parameter was smaller for MLM estimates, particularly in the case of λ_f estimated using this method (Figure 3.2).

Variance in the duration of bouts was significantly larger (Fligner-Killeen $\chi^2 =$ 50.9, 10.9, and 13.6, seals 1, 2, and 3, respectively; $P < 0.001$ all cases) when SDA with a 5 s bin width was used (Figure 3.3), except for one seal ($\chi^2 = 3.0$, $P = 0.08$; seal 4). Similar results were observed for postbout duration (Fligner-Killeen $\chi^2 =$ 22.2, 16.6, 25.2, and 18.2, seals 1, 2, 3, and 4 respectively; $P < 0.001$ all cases). Median duration of bouts (Wilcoxon $U = 654$, 1976, 6254, and 1220, $P < 0.05$, all cases), and postbout duration (Wilcoxon $U = 1327$, 1570, 6356, and 1048, $P < 0.05$, all cases) were also significantly larger when using SDA (Figure 3.3). The mean number of dives per bout was concomitantly smaller when using MLM (range: 7.4, 15.8), than when using SDA (range: 11.5, 20.1). Furthermore, the number of isolated dives varied from 158 to 323 when using MLM, whereas it varied from 54 to 170 when using SDA.

3.1.4 Discussion

There are several advantages to using the MLM approach for defining the BEC, compared to other methods. Langton et al. (1995) showed that it provides more precise parameter estimates than log-frequency analysis (Sibly et al. 1990) by using all the information in the data, and that methods based on log-frequency analysis may include some subjectivity in the choice of histogram bin widths, which form the basis of the model. Despite these advantages, MLM approaches remain unused for identifying foraging bouts, and dive bouts in particular, where methods based on log-frequency analysis are predominantly selected for this purpose. Our results support and extend the conclusions in Langton et al. (1995), and suggest that SDA (Mori et al. 2001) may be improved by using this approach.

Because the BEC is defined in terms of the parameters of a mixture of Poisson distributions, its accuracy depends on how well the fitted models describe observed data. The MLM estimates of the model performed better than SDA at describing the cumulative frequency distribution of t. This was evident with real data from all four randomly selected seals. In contrast, expected cumulative frequency distributions based on SDA estimates showed large deviations from observed data, resulting in serious overestimation of the number of interdive intervals within or between bouts. This condition was reproduced in the simulated data, and suggests it is a property of eq. (3.1) fit to the sequential absolute differences in interdive duration. Langton et al. (1995) found a bias in the opposite direction when fitting eq. (3.1) to the interval between events; i.e., $N_f + N_s$ was underestimated. These problems were avoided using MLM.

Differences between methods in their ability to predict observed cumulative frequencies were associated with large differences in estimated BECs. BECs determined through SDA were at least twice as large as BECs determined through MLM. Furthermore, simulated data suggest that BECs estimated through MLM are more accurate and precise than those estimated using log-frequency-based analyses. Such large differences between methods have not been previously shown, and the consequences for any study of foraging ecology based on diving behaviour can be important. Indeed, the number of bouts identified for each seal was considerably larger using MLM, providing finer temporal resolution of the animals' activity at sea. These differences lead to different interpretations of patch structure and characteristics (e.g., Boyd

1996, Harcourt et al. 2002, Mori and Boyd 2004*a*, Mori et al. 2005), where the BEC is used to determine different scales of foraging. Most notably, the temporal scale at which prey patches are encountered by the forager is smaller with the more accurate MLM approach.

Our results showed that increasing the bin widths for constructing the histograms required for identifying bouts based on log-frequency analysis result in larger BECs. A similar effect has been shown for identifying different scales of movement of ungulates (Johnson et al. 2006) using this technique. In our study, we varied the choice of bin width, from a minimum determined by the sampling resolution to 10 times this value, and found associated increases in BEC estimates of approximately 50% using the largest bin widths. There are no guidelines for choosing appropriate bin widths when using this approach, but Sibly et al. (1990) recommended increasing the bin width of longer, infrequent, intervals. However, using larger bin widths results in larger estimates of the BEC. Regardless of the method used for selecting the histogram bin widths, it is not clear what procedure was adopted in any particular analysis of dive bouts, as proxies of patch structure. Therefore, it is difficult to evaluate conclusions about scales of foraging, optimal diving behaviour, and prey patch quality.

Despite the increased accuracy and precision of the MLM approach, some departures from the model were observed. All model fits to real data resulted in underestimation of the cumulative frequency for high but non-asymptotic values of t (see eq. (3.1)) in all seals. Reasons for this departure are not clear with the available data, but may be related to the assumptions of the model. The distribution of intervals, or absolute differences between successive intervals, within each of the two Poisson processes is assumed to be random (Sibly et al. 1990). Therefore, the observed underestimations may indicate departures from this assumption. Large departures from a two-process model, similar to the one in eq. (3.1), have been documented for very brief and very long intervals between meals in dairy cows (Tolkamp et al. 1998). Tolkamp et al. (1998) argued that the departures could be explained by the cows' level of satiety, and proposed an alternative model to account for this effect. However, Tolkamp et al. (1998) studied the feeding behaviour of cows with almost unlimited access to food, which differs from conditions encountered by free-ranging fur seals and their prey. That departures from the model occurred only for $t >$ BEC supports this assertion. Therefore, it is difficult to assess the role of satiety levels in the departures from the model without independent measurements of prey ingestion, and distribution of prey patches.

The arguments and principles in favour of the MLM approach for identifying bouts not only apply to analyses of diving behaviour, but also to analyses of other foraging behaviours that are likely to reflect the spatiotemporal distribution of foraging patches (Wu and Loucks 1995). For instance, log-survivorship plots of the number of steps taken by kudus (*Tragelaphus strepsiceros* (Pallas, 1766)) (Owen-Smith and Novellie 1982) and by muskoxen (*Ovibos moschatus* (Zimmermann, 1780)) (Schaefer and Messier 1995) between feeding stations have been used to identify different scales of food patchiness. Johnson et al. (2002) used the same methods, considering movement rates between successive woodland caribou (*Rangifer tarandus caribou* (L., 1758)) location estimates as analogous to interdive durations in this study, and determined that ungulate movements within patches were strongly influenced by predation risk. Therefore, the improvements in accuracy achieved through MLM methods can bring new insights into foraging behaviour theory. In particular, accurately defining the time spent by animals in and between foraging patches is critical in models of optimal foraging (Stephens et al. 1986).

Whereas foraging behaviour bouts can provide a temporal proxy for foraging patches, the spatial location of those patches must be determined through animal movement data. Considerable efforts have been made to understand animal movement in relation to resource distribution, under the premise that animals move optimally through their habitat so as to maximize long-term energy intake rate (Fauchald 1999, Fortin 2002, Fauchald and Tveraa 2003, Klaassen et al. 2006). The concept of first-passage time; the time taken for an animal to cross a circle of a given radius along its path (Johnson et al. 1992), has been useful for defining spatial scales at which predators concentrate foraging effort (Fauchald and Tveraa 2003). Fauchald and Tveraa (2003) argued that the scale at which predators are most likely to display area-restricted search behaviour is equal to the radius at which variance in first-passage time is highest. However, this decision is based on the horizontal displacements of animals alone, and may not only reflect feeding activity (Robinson et al. 2007). Therefore, animal movement analysis techniques (e.g., first-passage time) combined with methods for accurate identification of behavioural bouts that can subsequently be attributed to foraging activities, may offer a better assessment of where and how animals exploit food resources.

The SDA procedure (Mori et al. 2001) improved upon previous methods of dive bout detection by removing the assumption of homogeneous dive bout characteristics. This assumption was considered inadequate, as animals may adjust their diving behaviour depending on the characteristics of the patch in which they forage (Mori et al. 2002, 2005). We suggest that the method can be further improved by adopting the MLM approach, which avoids the limitations associated with methods based on a histogram of observed data. Using this procedure to identify bouts based on other dive behaviour characteristics, in addition to differences in interdive duration (Mori et al. 2001), is possible, so more detailed information on foraging patches might be inferred. This approach may thus be a powerful tool to help understand foraging behaviour and prey patch characteristics more accurately.

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Table 3.1. Estimated parameters and bout ending criteria (BEC) (mean ± SE) from a model of sequential differences in interdive duration, using a maximum likelihood estimation method (MLM), and a log frequency analysis (SDA). Results from four different choices of bin widths (s) were used for the SDA approach. The number of dives observed for each seal is in parenthesis

	MLM[a]	SDA[b]			
		$5s$	$10s$	$20s$	$50s$
			Seal 1 (n = 1081)		
p	0.65 ± 0.025				
N_f		$3,070 \pm 477$	$6,480 \pm 1,300$	$13,500 \pm 3,800$	$36,700 \pm 15,600$
N_s		803 ± 95.7	$1,370 \pm 177$	$2,270 \pm 390$	$4,720 \pm 1220$
λ_f	0.069 ± 0.006	0.021 ± 0.003	0.020 ± 0.003	0.018 ± 0.003	0.016 ± 0.004
λ_s	0.005 ± 0.0003	0.002 ± 0.0002	0.002 ± 0.0003	0.002 ± 0.0003	0.002 ± 0.0004
BEC	51.1	191.2	209.6	249.6	289.3
Bouts	339	126	116	103	88
			Seal 2 (n = 910)		
p	0.63 ± 0.026				
N_f		$2,440 \pm 427$	$5,090 \pm 1,170$	$10,700 \pm 2,910$	$29,900 \pm 10,800$
N_s		$1,120 \pm 102$	$1,960 \pm 203$	$3,420 \pm 433$	$7,390 \pm 1,270$
λ_f	0.060 ± 0.004	0.023 ± 0.003	0.022 ± 0.004	0.019 ± 0.004	0.017 ± 0.004
λ_s	0.004 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0003
BEC	59.5	156.8	173.9	202.4	237.9
Bouts	320	186	168	146	139
			Seal 3 (n = 1881)		
p	0.74 ± 0.014				
N_f		$5,230 \pm 1,220$	$10,500 \pm 2,990$	$22,800 \pm 8,890$	$90,800 \pm 53,200$
N_s		$1,550 \pm 127$	$2,850 \pm 285$	$5,420 \pm 725$	$14,000 \pm 2,630$
λ_f	0.096 ± 0.004	0.047 ± 0.007	0.042 ± 0.008	0.041 ± 0.010	0.044 ± 0.014
λ_s	0.004 ± 0.0003	0.003 ± 0.0002	0.003 ± 0.0002	0.003 ± 0.0003	0.003 ± 0.0003
BEC	43.8	91.3	100.2	105.7	110.0
Bouts	478	287	276	270	270
			Seal 4 (n = 1164)		
p	0.80 ± 0.015				
N_f		$3,140 \pm 736$	$6,120 \pm 1,690$	$12,900 \pm 4,230$	$47,400 \pm 24,000$
N_s		906 ± 82	$1,530 \pm 152$	$2,760 \pm 303$	$6,570 \pm 1,050$
λ_f	0.083 ± 0.004	0.046 ± 0.007	0.038 ± 0.006	0.034 ± 0.007	0.036 ± 0.009
λ_s	0.004 ± 0.0003	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0003
BEC	56.6	96.7	118.9	134.8	140.9
Bouts	223	169	156	144	132

[a] The log likelihood function is shown in eq. (3.1)

[b] Columns represent four different bin choices of class interval width for fitting eq. (3.1)

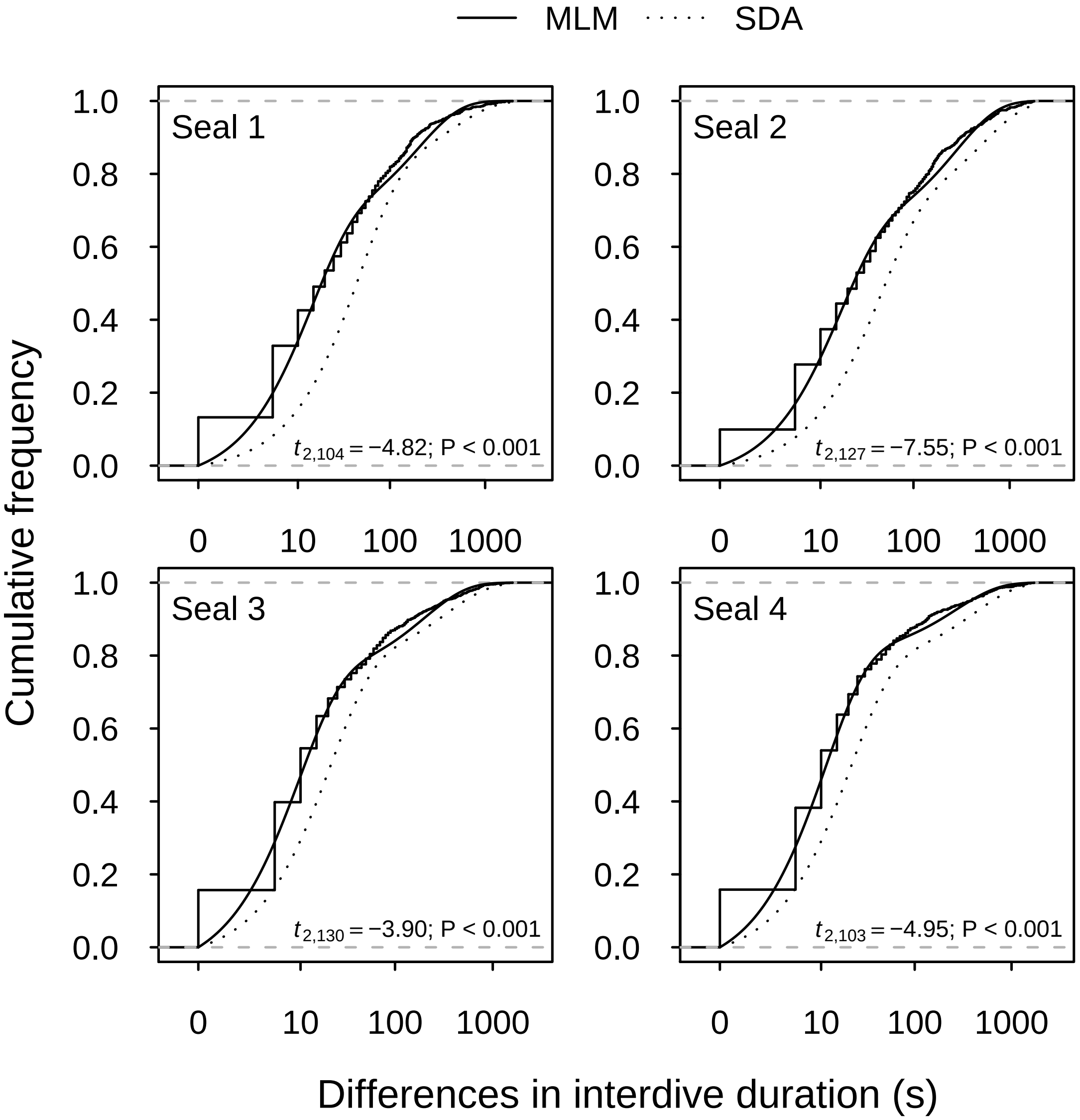

Figure 3.1. Relative cumulative frequencies (observed as a stepped function; estimated as the smooth lines) estimated through the maximum likelihood estimation method (MLM) were in better agreement with observed data than those estimated through log frequency analysis (SDA). A bin width of 5 s was used to fit the model through the log frequency analysis. Results of paired Student's *t*-tests comparing the squared residuals between models are also shown

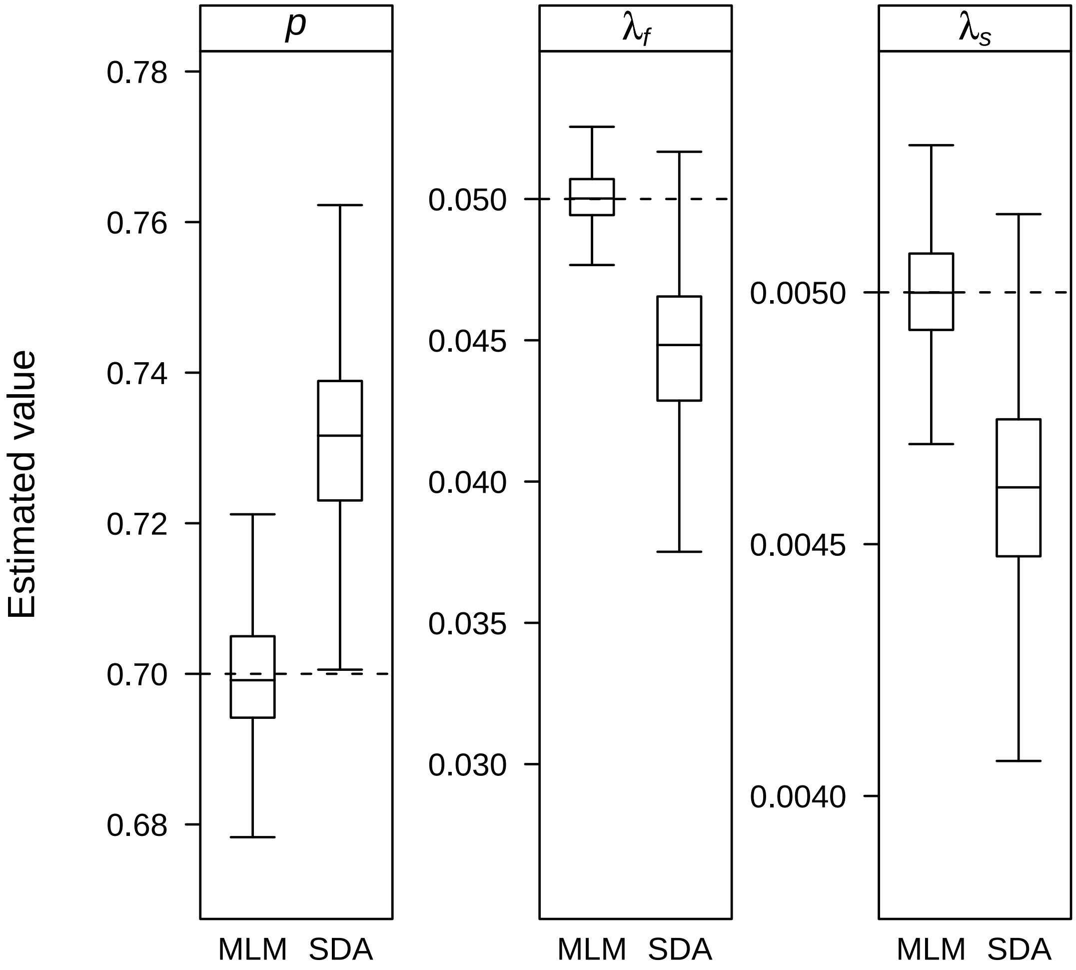

Figure 3.2. Bias of estimated parameters from 100 simulations of differences in interdive duration were smaller using the maximum likelihood estimation method (MLM), than with the histogram method (SDA). The median is indicated by the horizontal solid line; the interquartile range by the box; and the value that is, at most, 1.5 · interquartile range away from the box by the whiskers. The dashed lines indicate the true values of each parameter for all simulations

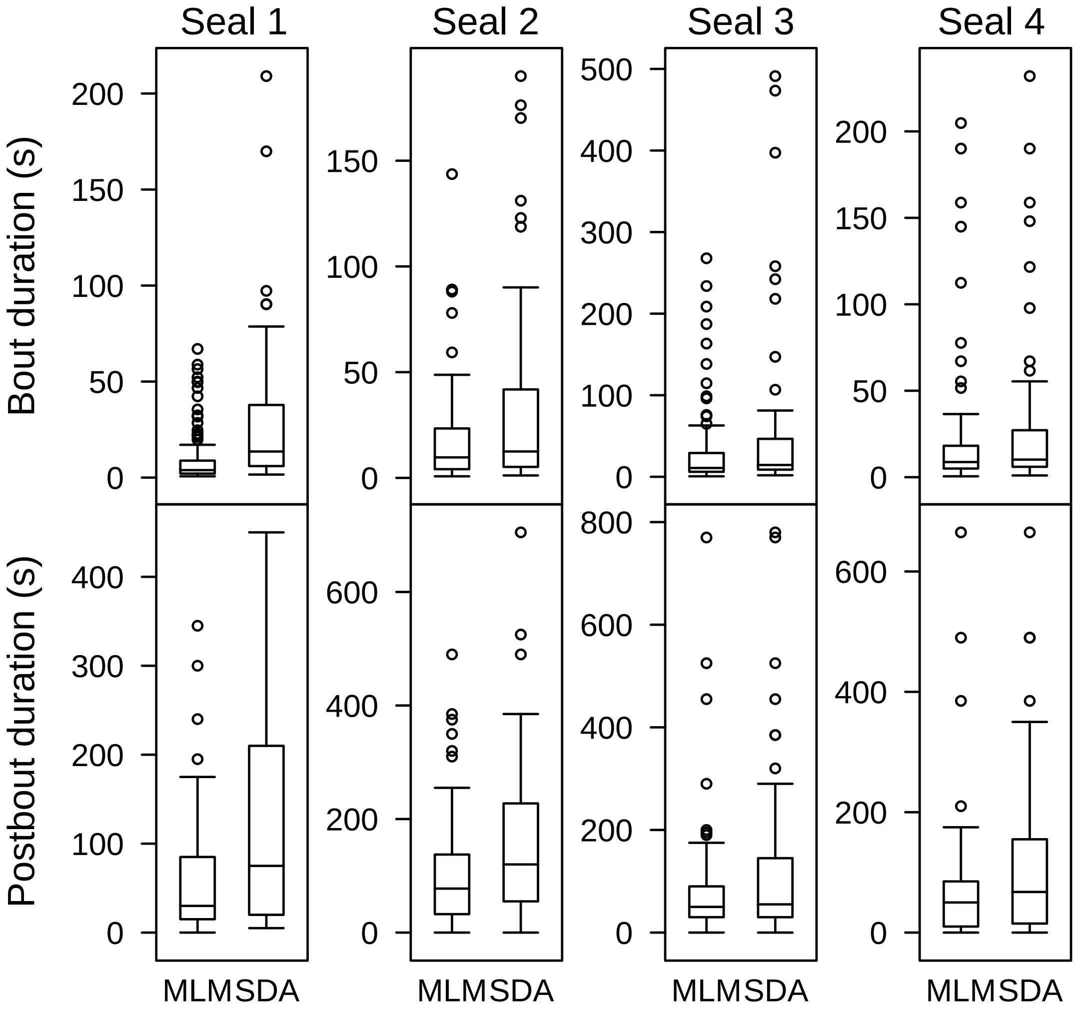

Figure 3.3. The median and variability of bout and postbout durations were significantly larger when using a log frequency analysis (SDA), compared to the maximum likelihood estimation method (MLM). Only bouts with at least 2 dives are shown. The median is indicated by the horizontal solid line; the interquartile range by the box; and the value that is, at most, 1.5 · interquartile range away from the box by the whiskers

A maximum likelihood approach for identifying dive bouts improves accuracy, precision and objectivity

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Summary

Foraging behaviour frequently occurs in bouts, and considerable efforts to properly define those bouts have been made because they partly reflect different scales of environmental variation. Methods traditionally used to identify such bouts are diverse, include some level of subjectivity, and their accuracy and precision is rarely compared. Therefore, the applicability of a maximum likelihood estimation method (MLM) for identifying dive bouts was investigated and compared with a recently proposed sequential differences analysis (SDA). Using real data on interdive durations from Antarctic fur seals (*Arctocephalus gazella* Peters, 1875), the MLM-based model produced briefer bout ending criterion (BEC) and more precise parameter estimates than the SDA approach. The MLM-based model was also in better agreement with real data, as it predicted the cumulative frequency of differences in interdive duration more accurately. Using both methods on simulated data showed that the MLM-based approach produced less biased estimates of the given model parameters than the SDA approach. Different choices of histogram bin widths involved in SDA had a systematic effect on the estimated BEC, such that larger bin widths resulted in longer BECs. These results suggest that using the MLM-based procedure with the sequential differences in interdive durations, and possibly other dive characteristics, may be an accurate, precise, and objective tool for identifying dive bouts.

Keywords: Antarctic fur seal, diving behaviour, foraging behaviour, foraging patch, pinniped.

Introduction

Many seabirds and marine mammals dive in bouts (Gentry et al., 1986; Huin & Prince, 1997; Kato et al., 2003); i.e., most of their dives occur in rapid

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succession, while the remaining are separated by longer intervals. Dives occurring in the same bout tend to resemble each other more than those occurring in different bouts. Based on their characteristics (e.g., mean dive depth and time spent at the bottom of the dive), bouts can be associated with a particular activity, such as travelling or foraging (Lea et al., 2002). Numerous studies use dive bouts to infer instances of a forager exploiting discrete prey patches (Boyd, 1996; Mori et al., 2002; Harcourt et al., 2002; Mori & Boyd, 2004a), because food resources are patchily distributed (Wroblewski et al., 1975; Croxall et al., 1985) at scales that organisms respond to (With & Crist, 1995; Wu & Loucks, 1995). Depending on the scale(s) at which food resources display patchiness (Wiens, 1976; Levin, 1992), the same argument is applied more generally to most animal behaviours associated with foraging, in both terrestrial (e.g., Schaefer & Messier, 1995; Munger, 1984; Rotenberry & Wiens, 1998) and aquatic environments (e.g., Kruuk et al., 1990; Fauchald, 1999). Therefore, it is essential to accurately and objectively identify behavioural bouts in studies of foraging ecology of aquatic and terrestrial predators. This can be achieved by determining a bout ending criterion (BEC), or how long an interval between two successive dives should be to assign them to different bouts.

The theory and methods used to determine the BEC have been reviewed elsewhere (Slater & Lester, 1982; Tolkamp & Kyriazakis, 1999). Events occurring in bouts are thought to be generated by a combination of two or more processes operating on progressively larger time scales. At the smallest scale, events are separated by similar and brief intervals. Events separated by markedly longer intervals define different groups of events (or bouts), thereby distinguishing the scale at which one process generates individual events from that generating bouts. Processes of both types are thought to follow a random Poisson distribution, where the intervals between them are described by a mixture of exponential distributions (Slater & Lester, 1982). Defining the BEC is, therefore, a problem of finding the time intervals that separate each process from the others.

Methods for searching the BEC include log-survivorship and log-frequency analysis (Gentry & Kooyman, 1986; Sibly et al., 1990). Boyd (1996) developed an iterative method to group dives into bouts by comparing the inter-dive duration of a given dive with the mean of those preceding it, considering it as part of a new bout if these values differed significantly. More recently, Mori et al. (2001) suggested another method, termed sequential differences analysis (SDA hereafter), based on log-frequency analysis. The BEC in this method could be estimated using the absolute differences between interdive durations, rather than the interdive durations themselves. If the occurrence of dives can be described by a mixture of Poisson distributions, the mean interdive duration should be the same for all bouts (Karlis & Xekalaki, 2005). However, in cases where dive bouts are considered as instances of a diver foraging in patches, interdive duration is expected to vary between bouts because it is closely related to dive depth (Houston & Carbone, 1992; Carbone & Houston, 1996; Boyd, 1997), which in turn depends on prey species composition and determines foraging patch quality for the predator (Thompson & Fedak, 2001). Mori et al. (2001), therefore, pointed out that previous methods may erroneously assume that mean interdive duration is common to all bouts; an assumption that can be avoided with SDA.

Although SDA has been useful in studies of foraging behaviour (Mori, 1998; Mori & Boyd, 2004b; Mori et al., 2005), it is based on fitting a nonlinear model to the logarithm of frequencies of absolute differences in interdive durations, and possibly other dive characteristics (e.g., dive depth). SDA relies on the construction of a histogram, using the midpoints of each class as the independent variable (Sibly et al., 1990). Therefore, a certain level of subjectivity is involved in the selection of class widths, and some information is lost by summarizing data from each class with a single value. Furthermore, class widths must be adjusted, or a weighting scheme must be implemented, to avoid empty classes. There are currently no objective criteria for dealing with these problems. Johnson et al. (2006) recently pointed out that the choices made throughout this procedure can have large influences on the BEC.

Some of these issues have been raised by Langton et al. (1995), and proposed to address them by using a maximum likelihood estimation method (MLM hereafter) for defining the BEC. This approach uses the information in the entire dataset of intervals between events. Unfortunately, the method has not been adopted to identify behavioural bouts in general, and dive bouts of marine predators in particular, where understanding spatiotemporal variation in prey distribution and quality is of major interest. Our aim was, therefore, to demonstrate the usefulness of this approach in this field, incorporating the concept used in SDA to avoid the assumption of invariant mean dive characteristics between dive bouts. We used time-depth recorder (TDR) data from lactating female Antarctic fur seals (*Arctocephalus gazella* Peters, 1875), during their foraging trips to sea, to compare models of the frequency of differences in interdive duration fit using SDA vs. those fit using MLM.

Methods

Data were obtained from lactating female Antarctic fur seals at La Mare aux Elephants (MAE; 46°22′29″S, 51°40′13″E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001-02 (4 December-25 March) and 2002-03 (1 December-16 March) breeding seasons.

Instrumentation and measurement of diving behaviour

Animal capture and handling procedures were described in Bailleul et al. (2005). Briefly, lactating females were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different time-depth recorder (TDR) models was glued to the dorsal fur between the scapulae, using a two-component glue (AW 2101 Ciba Specialty Chemicals): MK5, MK7, and MK8 (Wildlife Computers, Redmond, WA, USA). TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. Instruments were left on the seals for 1 to 11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals' return to the colony.

TDR data were downloaded to a portable computer, where analyses of the resulting time series of dive data were performed using custom written software, available as GNU R (R development Core Team, 2007) package diveMove (Luque, in press). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e., continuous depth readings) was available for at least 6 h. This limit was selected to exclude short excursions to sea for activities other than foraging, because these contained isolated shallow dives and mainly surface behaviour.

Dives were defined as departures from the surface to depths $\geqslant$ 4 m plus the ensuing return to surface. Dives to shallower depths were not considered because they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the instrument (Beck et al., 2000). Dives were, thus, described by their duration, maximal depth, and interdive duration.

For the purposes of this paper, data from the first recorded foraging trip to sea of four randomly selected individual seals were used in subsequent analyses. The models described below were fitted to each seal's dive record separately because foraging trip durations varied between them, and to avoid effects of interindividual variation in diving behaviour masking bout structure.

Identifying bouts using SDA

The variable used for defining bouts with SDA- and MLM-based methods was the absolute difference in interdive duration (t); the time between a dive and the preceding one. This procedure is based on a log-frequency analysis described in detail by Sibly et al. (1990) and further developed by Mori et al. (2001). Briefly, the first step of the method consists of creating a histogram of t, with the frequencies expressed as a logarithm. Because large values of t are considerably less frequent than small ones, some class intervals may have a frequency of zero, leading to the erroneous representation of frequencies in larger class intervals. To correct for this effect, the frequency of class intervals following intervals with zero frequency was divided by the number of preceding empty intervals plus one. The logarithm of the frequencies of all class intervals where frequency > 0 is, thus, considered a function of the midpoint of the intervals.

The distribution of t is assumed to be a mixture of two random Poisson processes; a fast and a slow one (Sibly et al., 1990). The fast process represents the small time scale at which individual dives occur, while the slow process represents the large time scale where bouts are distinguished. Therefore, the relationship described above can be defined as the sum of both processes:

$$y = \log[N_f \lambda_f e^{-\lambda_f t} + N_s \lambda_s e^{-\lambda_s t}] \qquad (1)$$

where y is the logarithm of the frequency of any given t; the subscripts $_f$ and $_s$ denote the fast and slow processes, respectively; N is the number of interdive intervals occurring in each process; and λ represents the probability of an event occurring in a given process per unit time (Sibly et al., 1990). Initial values for the N and λ parameters must be obtained in order to fit this negative exponential function. The broken-stick method was used for this purpose, following Sibly et al. (1990).

The BEC defining the threshold between the two Poisson processes can be obtained from equation (1):

$$BEC = \frac{1}{\lambda_f - \lambda_s} \log \frac{N_f \lambda_f}{N_s \lambda_s} \tag{2}$$

To assess the effect of the choice of histogram bin widths on the estimation procedure, the model was fit, and the BEC calculated using bin widths from 5 (i.e., the sampling resolution) to 50 s.

Identifying bouts using MLM

Langton et al. (1995) suggested that equation (1) did not consider that the total number of events observed should be equal to $N_f + N_s$, and, hence, that the model can be simplified by expressing one of these parameters as a function of the other. The authors presented also a maximum likelihood estimation method using all observed data, rather than a histogram of these, to describe the frequency of any given event. The log likelihood of all the N_t absolute differences in interdive duration can be expressed as:

$$\log L_2 = \sum_{i=1}^{N_t} \log[p\lambda_f e^{-\lambda_f t_i} + (1-p)\lambda_s e^{-\lambda_s t_i}] \tag{3}$$

where p is a mixing parameter representing the proportion of fast to slow process events in the sampled population. The parameters from equation (3) must be estimated numerically, hence an optimization procedure is required using appropriate initial values. These values were obtained by first maximizing a reparameterized version of equation (3) using a logit transformation of the p parameter, and a logarithm transformation of the λ parameters. Initial values for this reparameterized model were in turn calculated as for the SDA (i.e., by using the broken-stick method). Such transformations stabilized the variance in the parameters, and rescaled them to avoid difficulties with the optimization algorithm. The parameter estimates obtained from this procedure were untransformed, and used as initial values for maximizing equation (3). Therefore, parameter estimates and their standard errors were obtained in their original scales.

The BEC in this case was estimated analogously to equation (2):

$$BEC = \frac{1}{\lambda_f - \lambda_s} \log \frac{p\lambda_f}{(1-p)\lambda_s} \tag{4}$$

Comparison between methods

Models describing the distribution of interdive differences in dive duration (t) should accurately predict t's relative cumulative frequency. The expected relative cumulative frequency (f_c) of t can be calculated from parameters in models (1) and (3) using:

$$f_c = 1 - pe^{-\lambda_f t} - (1-p)e^{-\lambda_s t} \tag{5}$$

Thus, f_c for the range of observed t, and the actual relative cumulative frequency distribution of t were also calculated. The observed and expected relative cumulative frequencies of t were plotted simultaneously against t (logarithmically transformed) to compare the fit of the two models to data, as proposed by Langton et al. (1995). Differences in model outcomes, relative to observed cumulative frequencies, were tested by comparing the squared residuals (observed – predicted values, squared) between the models with a paired Student's t-test (Zar, 1996).

Standard errors (SEs) for each parameter estimate provided a measure of the precision of each fitted model, and hence that of the estimated BEC. Bias was compared using simulated data generated with chosen mixing (p) and probability (λ) parameters. Based on the mid-range of observed data for all four seals, the mixing parameter was set to 0.7, and values for the probability parameters were set to 0.05 and 0.005 (λ_f and λ_s, respectively). Thus, one thousand values for t were simulated 100 times with these values, by generating a mixture of two random samples with exponential distribution ($f(\lambda_x, t) = \lambda_x e^{-\lambda_x t}$): one with $\lambda_x = 0.05$ if a random uniform variable x ($1 \geqslant x \geqslant 0$) from the total of 100 was <0.7, and another with $\lambda_x = 0.005$ otherwise. Each simulated mixture was fit with both models, using the respective methods described above. The bias of the estimates in the simulations, with respect to the true value for the parameters, were subsequently calculated and compared. All data manipulations and computations were done in the GNU R statistical system and programming language (R development Core Team, 2007).

To compare the effect of each method on interpretations of the behaviour of study animals, each seal's dive record was divided into bouts using the estimated BECs. The mean and variance of bout duration and interval between bouts was calculated and compared between models for each seal using Wilcoxon rank-sum and Fligner–Killeen tests, respectively (Conover et al., 1981).

Results

The number of dives observed for each seal varied from 910 to 1881 (Table 1). Probability parameter (λ) estimates from these samples were larger using MLM compared to those obtained through SDA. Conversely, the mixing parameter (p) was consistently smaller using MLM, and the total number of interdive intervals ($N_f + N_s$) was largely overestimated using SDA. As a result of these differences, estimated BECs were markedly larger using SDA, by factors ranging from 2 to 6 (Table 1). SEs of estimated parameters were generally smaller using MLM. More importantly, the total number of bouts identified for each seal was considerably smaller when using SDA (Table 1).

Varying the bin width for creating the histograms used in SDA resulted in systematic changes in most parameters: estimated BECs and numbers of interdive intervals (N_f and N_s) increased, but λ_f tended to decrease. SEs of estimated parameters increased as class bin widths were increased (Table 1). Using the narrowest bin width for the sampling interval programmed for TDRs (5 s), variation in estimated BECs among seals was larger using SDA (range 91.3-191.2 s) than MLM (range 43.8-59.5 s).

Estimated and observed cumulative frequencies differed for high but non-asymptotic t values, regardless of the model (Figure 1). However, such departures were larger for models fit through SDA. Models fit through MLM followed the observed cumulative frequencies more closely, although they underestimated these frequencies for large t values (Figure 1). The sum of squared residuals from MLM-derived frequencies (relative to observed) ranged from 0.06 to 0.09, and from 0.5 to 1.0 for SDA-derived frequencies. The difference between models was significant for all seals (Figure 1).

Bias of estimated parameters from models of simulated t values were 0.001, 0.0002, 0.00002 when fit through MLM, and 0.031, -0.0028, -0.0010 when fit through SDA (p, λ_f, λ_s, respectively). Thus, biases were smaller, and variation for each parameter was smaller for MLM estimates, particularly in the case of λ_f estimated using this method (Figure 2).

Table 1. Estimated parameters and bout ending criteria (BEC) (mean ± SE) from a model of sequential differences in interdive duration, using a maximum likelihood estimation method (MLM), and a log frequency analysis (SDA). Results from four different choices of bin widths (s) were used for the SDA approach. The number of dives observed for each seal is in parenthesis.

	MLM[a]	SDA[b]			
		5 s	10 s	20 s	50 s
Seal 1 ($N = 1081$)					
p	0.65 ± 0.025				
N_f		3070 ± 477	6480 ± 1300	13 500 ± 3800	36 700 ± 15 600
N_s		803 ± 95.7	1370 ± 177	2270 ± 390	4720 ± 1220
λ_f	0.069 ± 0.006	0.021 ± 0.003	0.020 ± 0.003	0.018 ± 0.003	0.016 ± 0.004
λ_s	0.005 ± 0.0003	0.002 ± 0.0002	0.002 ± 0.0003	0.002 ± 0.0003	0.002 ± 0.0004
BEC	51.1	191.2	209.6	249.6	289.3
Bouts	339	126	116	103	88
Seal 2 ($N = 910$)					
p	0.63 ± 0.026				
N_f		2440 ± 427	5090 ± 1170	10 700 ± 2910	29 900 ± 10 800
N_s		1120 ± 102	1960 ± 203	3420 ± 433	7390 ± 1270
λ_f	0.060 ± 0.004	0.023 ± 0.003	0.022 ± 0.004	0.019 ± 0.004	0.017 ± 0.004
λ_s	0.004 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0003
BEC	59.5	156.8	173.9	202.4	237.9
Bouts	320	186	168	146	139
Seal 3 ($N = 1881$)					
p	0.74 ± 0.014				
N_f		5230 ± 1220	10 500 ± 2990	22 800 ± 8890	90 800 ± 53 200
N_s		1550 ± 127	2850 ± 285	5420 ± 725	14 000 ± 2630
λ_f	0.096 ± 0.004	0.047 ± 0.007	0.042 ± 0.008	0.041 ± 0.010	0.044 ± 0.014
λ_s	0.004 ± 0.0003	0.003 ± 0.0002	0.003 ± 0.0002	0.003 ± 0.0003	0.003 ± 0.0003
BEC	43.8	91.3	100.2	105.7	110.0
Bouts	478	287	276	270	270
Seal 4 ($N = 1164$)					
p	0.080 ± 0.015				
N_f		3140 ± 736	6120 ± 1690	12 900 ± 4230	47 400 ± 24 000
N_s		906 ± 82	1530 ± 152	2760 ± 303	6570 ± 1050
λ_f	0.083 ± 0.004	0.046 ± 0.007	0.038 ± 0.006	0.034 ± 0.007	0.036 ± 0.009
λ_s	0.004 ± 0.0003	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0003
BEC	56.6	96.7	118.9	134.8	140.9
Bouts	223	169	156	144	132

[a] The log likelihood function is shown in equation (3).

[b] Columns represent four different choices of class interval width for fitting equation (1).

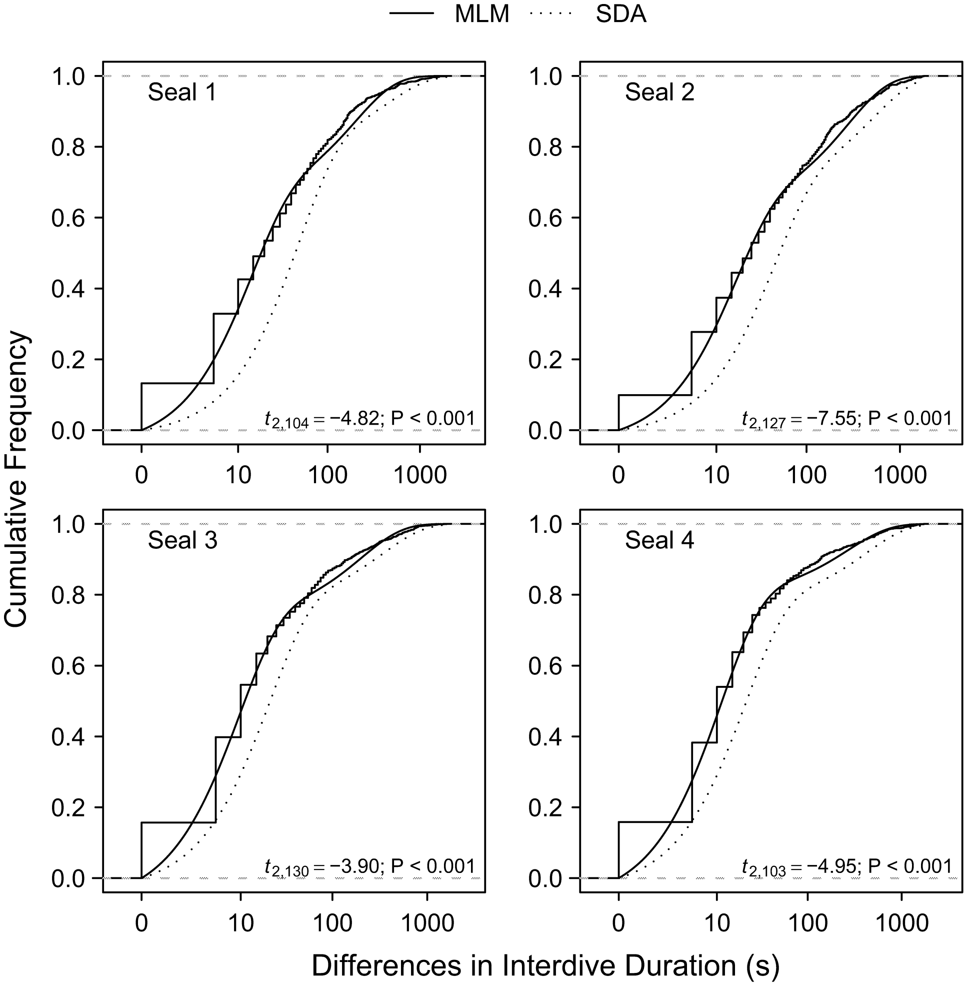

Figure 1. Relative cumulative frequencies (observed as a stepped function; estimated as the smooth lines) estimated through the maximum likelihood estimation method (MLM) were in better agreement with observed data than those estimated through log frequency analysis (SDA). A bin width of 5 s was used to fit the model through the log frequency analysis. Results of paired Student's t-tests comparing the squared residuals between models are also shown.

Variance in the duration of bouts was significantly larger (Fligner–Killeen $\chi^2 = 50.9, 10.9$ and 13.6, seals 1, 2 and 3, respectively; $p < 0.001$ all cases) when SDA with a 5 s bin width was used (Figure 3), except for one seal ($\chi^2 = 3.0$, $p = 0.08$; seal 4). Similar results were observed for postbout duration (Fligner–Killeen $\chi^2 = 22.2, 16.6, 25.2$ and 18.2, seals 1, 2, 3 and 4, respectively; $p < 0.001$, all cases). Median duration of bouts (Wilcoxon

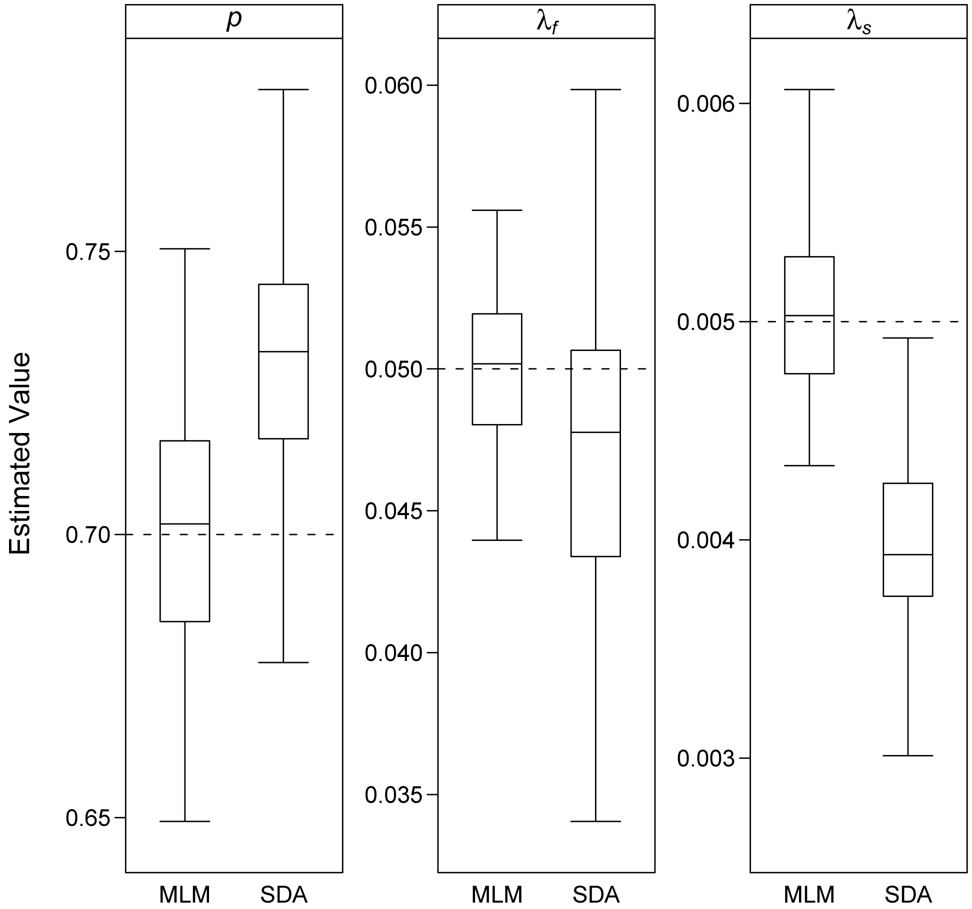

Figure 2. Bias of estimated parameters from 100 simulations of differences in interdive duration were smaller using the maximum likelihood estimation method (MLM), than with the histogram method (SDA). The median is indicated by the horizontal solid line; the interquartile range by the box; and the value that is, at most, 1.5 · interquartile range away from the box by the whiskers. The dashed lines indicate the true values of each parameter for all simulations.

$U = 654$, 1976, 6254 and 1220, $p < 0.05$, all cases) and postbout duration (Wilcoxon $U = 1327$, 1570, 6356 and 1048, $p < 0.05$, all cases) were also significantly larger when using SDA (Figure 3). The mean number of dives per bout was concomitantly smaller when using MLM (range 7.4-15.8), than when using SDA (range 11.5-20.1). Furthermore, the number of isolated dives varied from 158 to 323 when using MLM, whereas it varied from 54 to 170 when using SDA.

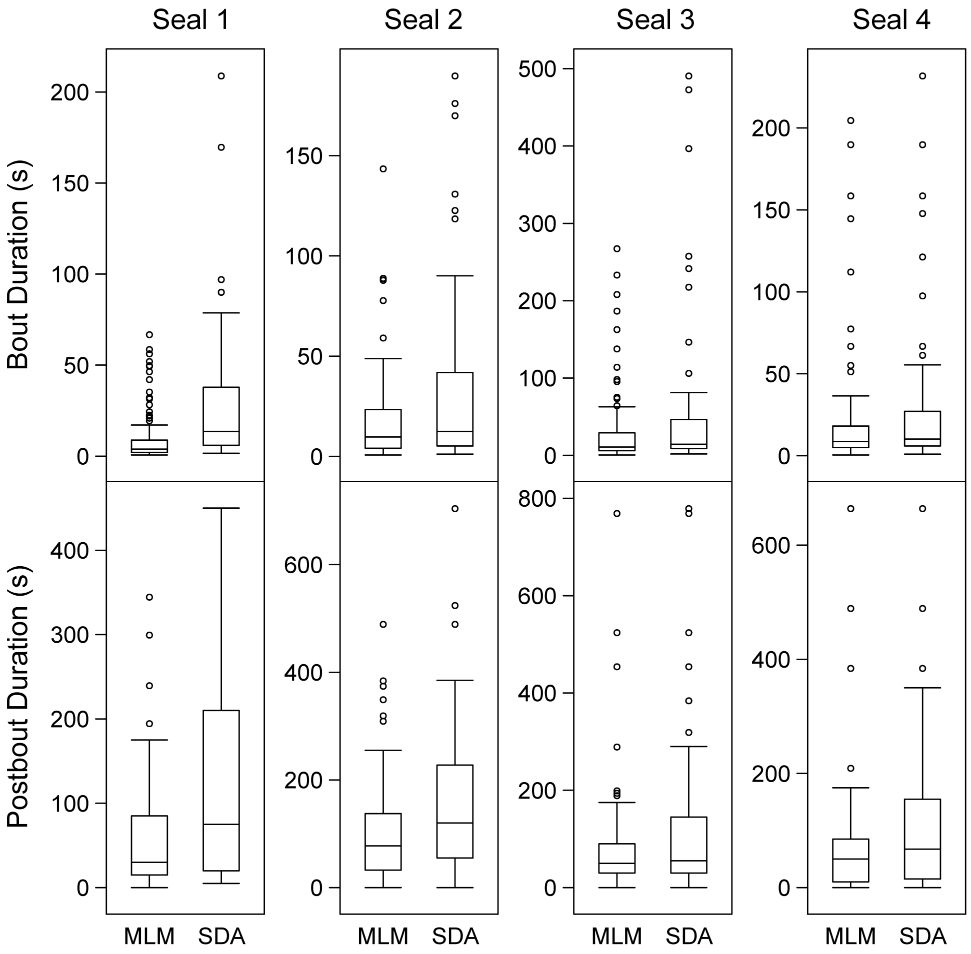

Figure 3. The median and variability of bout and postbout durations were significantly larger when using a log frequency analysis (SDA), compared to the maximum likelihood estimation method (MLM). Only bouts with at least 2 dives are shown. The median is indicated by the horizontal solid line; the interquartile range by the box; and the value that is, at most, 1.5 · interquartile range away from the box by the whiskers.

Discussion

There are several advantages to using the MLM approach for defining the BEC, compared to other methods. Langton et al. (1995) showed that it provides more precise parameter estimates than log-frequency analysis (Sibly et al., 1990) by using all the information in the data, and that methods based on log-frequency analysis may include some subjectivity in the choice of histogram bin widths, which form the basis of the model. Despite these advantages, MLM approaches remain unused for identifying foraging bouts, and dive bouts in particular, where methods based on log-frequency analysis are predominantly selected for this purpose. Our results support and extend the conclusions in Langton et al. (1995), and suggest that SDA (Mori et al., 2001) may be improved by using this approach.

Because the BEC is defined in terms of the parameters of a mixture of Poisson distributions, its accuracy depends on how well the fitted models describe observed data. The MLM estimates of the model performed better than SDA at describing the cumulative frequency distribution of t. This was evident with real data from all four randomly selected seals. In contrast, expected cumulative frequency distributions based on SDA estimates showed large deviations from observed data, resulting in serious overestimation of the number of interdive intervals within or between bouts. This condition was reproduced in the simulated data, and suggests it is a property of equation (1) fit to the sequential absolute differences in interdive duration. Langton et al. (1995) found a bias in the opposite direction when fitting equation (1) to the interval between events; i.e., $N_f + N_s$, was underestimated. These problems were avoided using MLM.

Differences between methods in their ability to predict observed cumulative frequencies were associated with large differences in estimated BECs. BECs determined through SDA were at least twice as large as BECs determined through MLM. Furthermore, simulated data suggest that BECs estimated through MLM are more accurate and precise than those estimated using log-frequency-based analyses. Such large differences between methods have not been previously shown, and the consequences for any study of foraging ecology based on diving behaviour can be important. Indeed, the number of bouts identified for each seal was considerably larger using MLM, providing finer temporal resolution of the animals' activity at sea. These differences lead to different interpretations of patch structure and characteristics (e.g., Boyd, 1996; Harcourt et al., 2002; Mori & Boyd, 2004a; Mori et al., 2005), where the BEC is used to determine different scales of foraging. Most notably, the temporal scale at which prey patches are encountered by the forager is smaller with the more accurate MLM approach.

Our results showed that increasing the bin widths for constructing the histograms required for identifying bouts based on log-frequency analysis result in larger BECs. A similar effect has been shown for identifying different scales of movement of ungulates (Johnson et al., 2006) using this technique. In our study, we varied the choice of bin width, from a minimum determined by the sampling resolution to 10 times this value, and found associated increases in BEC estimates of approximately 50% using the largest bin widths. There are no guidelines for choosing appropriate bin widths when using this approach, but Sibly et al. (1990) recommended increasing the bin width of longer, infrequent, intervals. However, using larger bin widths resulted in larger estimates of the BEC. Regardless of the method used for selecting the histogram bin widths, it is not clear what procedure was adopted in any particular analysis of dive bouts, as proxies of patch structure. Therefore, it is difficult to evaluate conclusions about scales of foraging, optimal diving behaviour, and prey patch quality.

Despite the increased accuracy and precision of the MLM approach, some departures from the model were observed. All model fits to real data resulted in underestimation of the cumulative frequency for high but non-asymptotic values of t (see equation (1)) in all seals. Reasons for this departure are not clear with the available data, but may be related to the assumptions of the model. The distribution of intervals, or absolute differences between successive intervals, within each of the two Poisson processes is assumed to be random (Sibly et al., 1990). Therefore, the observed underestimations may indicate departures from this assumption. Large departures from a two-process model, similar to the one in equation (1), have been documented for very brief and very long intervals between meals in dairy cows (Tolkamp et al., 1998). Tolkamp et al. (1998) argued that the departures could be explained by the cows' level of satiety, and proposed an alternative model to account for this effect. However, Tolkamp et al. (1998) studied the feeding behaviour of cows with almost unlimited access to food, which differs from conditions encountered by free-ranging fur seals and their prey. That departures from the model occurred only for $t > \text{BEC}$ supports this assertion. Therefore, it is difficult to assess the role of satiety levels in the departures from the model without independent measurements of prey ingestion, and distribution of prey patches.

The arguments and principles in favour of the MLM approach for identifying bouts not only apply to analyses of diving behaviour, but also to analyses of other foraging behaviours that are likely to reflect the spatiotemporal distribution of foraging patches (Wu & Loucks, 1995). For instance, log-survivorship plots of the number of steps taken by kudus (*Tragelaphus strepsiceros* Pallas, 1766) (Owen-Smith & Novellie, 1982) and by muskoxen

(*Ovibos moschatus* Zimmermann, 1780) (Schaefer & Messier, 1995) between feeding stations have been used to identify different scales of food patchiness. Johnson et al. (2002) used the same methods, considering movement rates between successive woodland caribou (*Rangifer tarandus caribou* Linnaeus, 1758) location estimates as analogous to interdive durations in this study, and determined that ungulate movements within patches were strongly influenced by predation risk. Therefore, the improvements in accuracy achieved through MLM methods can bring new insights into foraging behaviour theory. In particular, accurately defining the time spent by animals in and between foraging patches is critical in models of optimal foraging (Stephens et al., 1986).

Whereas foraging behaviour bouts can provide a temporal proxy for foraging patches, the spatial location of those patches must be determined through animal movement data. Considerable efforts have been made to understand animal movement in relation to resource distribution, under the premise that animals move optimally through their habitat so as to maximize long-term energy intake rate (Fauchald, 1999; Fortin, 2002; Fauchald & Tveraa, 2003; Klaassen et al., 2006). The concept of first-passage time; the time taken for an animal to cross a circle of a given radius along its path (Johnson et al., 1992), has been useful for defining spatial scales at which predators concentrate foraging effort (Fauchald & Tveraa, 2003). Fauchald & Tveraa (2003) argued that the scale at which predators are most likely to display area-restricted search behaviour is equal to the radius at which variance in first-passage time is highest. However, this decision is based on the horizontal displacements of animals alone, and may not only reflect feeding activity (Robinson et al., 2007). Therefore, animal movement analysis techniques (e.g., first-passage time) combined with methods for accurate identification of behavioural bouts that can subsequently be attributed to foraging activities, may offer a better assessment of where and how animals exploit food resources.

The SDA procedure (Mori et al., 2001) improved upon previous methods of dive bout detection by removing the assumption of homogeneous dive bout characteristics. This assumption was considered inadequate, as animals may adjust their diving behaviour depending on the characteristics of the patch in which they forage (Mori et al., 2002, 2005). We suggest that the method can be further improved by adopting the MLM approach, which avoids the limitations associated with methods based on a histogram of observed data. Using this procedure to identify bouts based on other dive behaviour characteristics, in addition to differences in interdive duration (Mori et al., 2001), is possible, so more detailed information on foraging patches might be inferred. This approach may, thus, be a powerful tool to help understand foraging behaviour and prey patch characteristics more accurately.

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3.2 Temporal structure of diving behaviour in sympatric Antarctic and subantarctic fur seals

Abstract

Lactation is considerably briefer (4 vs. 10 months) and daily pup energy expenditure is higher in Antarctic (AFS, *Arctocephalus gazella* (Peters, 1875)) than in subantarctic (SFS, *Arctocephalus tropicalis* (Gray, 1872)) fur seals, even in sympatric populations of both species, where their foraging locations and diets are similar. Therefore, lactational demands may be higher for AFS females. We investigated whether sympatric lactating AFS and SFS fur seal females differ in their physiological or behavioural diving capacities, and in the temporal structure of foraging behaviour. Mean dive depth and duration were larger in SFS, but dives below 130 m were performed only by AFS. An index of the activity level during the bottom phase of dives, when fur seals are thought to capture prey, was higher in SFS. Despite these differences, SFS females showed a steady increase in the minimum post-dive interval following dives lasting longer than 250 s, compared to 150 s in AFS. These results suggest that physiological constraints on diving behavior are stronger on AFS females, and that behavioural aerobic dive limit is greater for SFS. Assuming that dive bouts reflect foraging in prey patches, AFS females exploited more patches per unit time, and remained in them for briefer periods of time, compared to SFS females. Dive bout structure did not differ between overnight and long foraging trips. Our data suggest that AFS females spend greater effort foraging, but may gain access to prey patches of better quality, which may help them cope with higher lactational demands.

3.2.1 Introduction

Exploitative competition for food between animals is difficult to assess, partly because it requires knowledge of whether the level of their common resources is limiting or not (Birch 1957, MacArthur and Levins 1964). Yet it is considered a major component of species interactions, and influences community structure (Milinski and Parker 1991). In the absence of data on the level of common resources, it is often inferred from measurements of resource overlap or manipulations of population densities (Schoener 1974). However, an approach based on comparisons of the biology and behaviour of the potentially competing species may be more useful for understanding interspecific interactions (Tilman 1987). This approach has been used to study mechanisms of coexistence in a broad range of species (Stamps 1983, Cowlishaw 1999, Hull 1999, Robinson et al. 2002).

Using this approach, Ballance et al. (1997) showed that competitive ability and energetic constraints play a major role in the structure of seabird assemblages. Cases where morphologically similar, related, species occur in sympatry or syntopy are particularly attractive for studying these interactions. Under such conditions, it is possible to compare the ecology of co-occurring species, while minimizing the influence of extraneous factors, which are difficult or impossible to control for. Studies of related seabirds have provided evidence of physiological constraints on the behavioural response of coexisting predators to heterogeneity in the distribution of common prey resources (Hull 1999, Mori and Boyd 2004*b*). Therefore, they can be used as the basis for predicting the outcome of reductions in prey abundance and/or availability.

Lactation constrains the foraging behaviour of mammals (Sæther and Gordon 1994), especially in the marine environment (Costa and Williams 1999). Therefore, new insights into the mechanisms linking prey distribution and predator behaviour can be gained by comparing the foraging behaviour of sympatric marine mammals. Otariid (fur seals and sea lions) pinnipeds are good models in comparative foraging ecology because they exhibit large variation in adult body size and lactation duration, while other life history traits are relatively homogeneous (Ridgway and Harrison 1981). Female body mass varies from ~30 (Galápagos fur seals, *Arctocephalus galapagoensis* (Heller, 1904)) to 275 kg (Steller sea lions, *E. jubatus*), and lactation duration varies from 4 (Antarctic fur seal, *Arctocephalus gazella* (Peters, 1875)) to 36 months (Galápagos fur seals; range: 12-36 months (Trillmich and Kooyman 1986)). Large pinnipeds have higher aerobic dive limits (ADLs) than smaller ones (Kooyman 1989), so they can dive for longer periods of time (Halsey et al. 2006) without the negative effects of increased concentration of lactic acid. Consequently, they have more time available to search for and capture prey. However, species of similar body mass can display large differences in lactation duration, energy transfer to pups, and patterns of energy allocation by pups (Arnould 1997, Arnould et al. 2003). Therefore, the interplay between body mass, foraging behaviour, and lactation duration remain unclear. Sympatric otariids of similar body mass, yet different lactation duration, offer a unique opportunity to understand what physiological and behavioural tradeoffs breeding females face during lactation.

Diving marine predators often dive in bouts, i.e. most dives occur in rapid succession, while the rest are separated by longer intervals, and each bout may indicate foraging in a particular patch (Mori and Boyd 2004*a*). Researchers thus deduced that the temporal structure of diving may be used to infer the distribution and characteristics of foraging patches in several seabirds (Kato et al. 2000, Mehlum et al. 2001), and pinnipeds (Mori and Boyd 2004*a*, Mori et al. 2005). This provides a framework on which to compare the foraging behaviour of sympatric marine mammals in relation to a common prey resource.

Antarctic and subantarctic (*A. tropicalis* (Gray, 1872) fur seals (AFS and SFS, respectively, hereafter) have broadly different spatial distributions. AFS breed mostly south of the Antarctic Polar Front, while SFS breed mostly north of it, but they breed sympatrically at three locations (Bonner 1999): Macquarie Island, Ile de la Possession (Iles Crozet), and Marion Island (Prince Edward Islands). Adult females of these species have similar body mass, and show little differences in at-sea distribution and diet when in sympatry (Klages and Bester 1998, Robinson et al. 2002, Bailleul et al. 2005, Luque et al. 2007*a*), yet pups are weaned at 4 vs. 10 months of age in AFS and SFS (Bester and Bartlett 1990), respectively, as they are in allopatric populations. Furthermore, AFS pups showed higher daily energy expenditures (Arnould et al. 2003), and also grow faster in body length (Luque et al. 2007*b*) at Ile de la Possession. Therefore, their mothers must meet these demands in addition to their own, and also complete lactation in less than one half the time available to SFS. Lactational demands may thus be higher in AFS, which females should satisfy during their foraging trips to sea.

Previous comparisons of diving behaviour between these species in sympatry have not shown major differences at the scale of entire foraging trips (Goldsworthy et al. 1997, Robinson et al. 2002). At Ile de la Possession, however, overnight foraging trips (OFTs) are significantly more frequent in SFS, and as in Marion Island, AFS appear to spend a greater proportion of their time at sea (Bester and Bartlett 1990, Bailleul et al. 2005, Luque et al. 2007*a*). Differences at finer scales have been studied at Ile de la Possession, where lactating female AFS exhibit stronger diel variation in dive depth, with relatively shallow (AFS: 25-30 m; SFS: 35-50 m) diving during the noncrepuscular hours of the night, and deep (AFS: 45-65 m; SFS: 40-50 m) diving during crepuscular hours (Luque et al. 2007*a*). At Marion Island (Klages and Bester 1998, Ferreira and Bester 1999) and Macquarie Island (Robinson et al. 2002), no interspecific differences in diet were found. Scat analyses suggest that sympatric AFS and SFS feed on the same prey species (myctophid fish), although differences in their relative abundance were found at Ile de la Possession (Luque et al. 2007*a*). Comparisons of the temporal structure of diving behaviour between AFS and SFS, however, are unavailable, but may help understand how these species with different lactational demands respond to distribution of similar prey.

Diving capacity of otariid species with similar body mass is expected to be similar (Kooyman 1989), assuming other factors do not differ. In this case, optimal diving models predict that their optimal foraging depth should be similar (Mori 1998*a*, 2002). Optimal diving models typically assume that divers maximize energy intake rate, although predation risk may significantly influence such predictions (Frid et al. 2007). They also predict that divers should increase the time spent in foraging patches as depth increases (Mori 1998*b*, Thompson and Fedak 2001), but only if diving remains aerobic (Houston and Carbone 1992) or patch quality (as reflected by prey density) increases. A previous study does not support the first prediction (Luque et al. 2007*a*), suggesting that important physiological or behavioural differences exist between female AFS and SFS, which may affect how they exploit prey patches. Therefore, we investigated whether the temporal structure of diving behaviour and vertical distribution of foraging patches differ between fur seal species at Ile de la Possession. Given the shorter lactation and higher daily energy requirements of AFS pups, we assessed the hypothesis that female AFS have higher energy demands during lactation, so they should spend more effort foraging, despite their overlapping foraging areas.

3.2.2 Materials and methods

Data on diving behaviour of AFS and SFS was obtained at La Mare aux Elephants (46°22'29" S, 51°40'13" E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001-02 (4 December - 25 March) and 2002-03 (1 December - 16 March) breeding seasons (2001 and 2002 hereafter). A total of 277 (AFS: 153, SFS: 124) pups were individually marked as previously described (Georges and Guinet 2000*a*, Arnould et al. 2003, Bailleul et al. 2005), providing a means to identify their mothers, a subset of which were instrumented with time and depth recorders (time-depth recorders (TDRs); Table 3.2).

Instrumentation and measurement of diving behaviour

Animal capture and handling procedures were described in Luque et al. (2007*a*). Briefly, lactating females of each species were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different TDR models was glued to the dorsal fur between the scapulae, using a two-component glue (AW 2101 Ciba Specialty Chemicals): MK5, MK7, and MK8 (Wildlife Computers, Redmond, Washington, U.S.A.). Fur seals travelled 50 to 100 km from the colony to forage, and there were no significant differences in foraging trip duration, dive depth, nor dive duration between animals instrumented with different TDR models ($P > 0.5$ in all cases). Therefore, data from the 3 models were pooled for interspecific comparison purposes. TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. MK8 TDRs also recorded speed to the nearest $0.02 \text{ m} \cdot \text{s}^{-1}$. Instruments were left on the seals for 1 to 11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals' return to the colony.

TDR data were downloaded to a portable computer, and analyses of the resulting time series of dive data were performed using custom written software, available through GNU R (R development Core Team 2007) package `diveMove` (Luque 2007). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e. continuous depth readings) was available for at least 6 h. This limit was selected to exclude short excursions to sea for activities other than foraging, because they occurred mostly during daytime, and contained isolated shallow (< 20 m) dives, which contrasted with the bout-organized dives typical of foraging trips (Luque et al. 2007*a*).

Dives were defined as departures from the surface to depths ≥ 4 m plus the ensuing return to the surface. Dives to lower depths were not considered, as they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the instrument (Beck et al. 2000). Each dive was divided into descent, bottom, and ascent phases, where: (1) descent started at the surface and ended when no further increases in depth were detected; (2) ascent was defined from the end of the dive and, with the reversed time series, ending when no further increases in depth were detected; and (3) the bottom was the period between descent and ascent phases. Dives were thus described by their duration, maximal depth, bottom time, and postdive duration.

Fur seals catch their prey predominantly during the bottom phase of dives, although it has been demonstrated only for AFS (Hooker et al. 2002). Therefore, we calculated the absolute number of vertical meters each individual swam during this phase divided by bottom time, as a measure of the level of activity during the bottom (foraging) phase of dives. We also calculated mean swimming speed during the bottom phase of dives from fur seals deployed with MK8 TDRs. Speed measurements do not correspond to true speed because they need to be calibrated against true speed of the seals. However, we were interested in comparing the level of activity during the bottom phase of dives between species, rather than estimating true speed, so measured speed was used as an index of such levels for the purposes of this study.

To investigate whether physiological constraints differ between species, we studied the relationship between the briefest postdive duration and dive duration binned at 5 s intervals. The dive duration beyond which the briefest postdive interval begins to rise was taken as a behavioural proxy for the ADL; the dive duration beyond which blood lactate levels rise, as a result of increasing anaerobic metabolism (Kooyman 1989).

Identification of dive bouts

Identification of bouts of most behaviours has traditionally relied on log-survivorship or log-frequency analysis (Gentry and Kooyman 1986*b*, Sibly et al. 1990). However, Langton et al. (1995) pointed out that these methods included some level of subjectivity, because they are based on fitting a curve to histogram data. The procedure involves an arbitrary choice of histogram class width, and adjustment for empty class intervals. Langton et al. (1995) presented an improved approach, based on Maximum Likelihood estimation, which uses the entire dataset to describe the frequency distribution of events such as diving. This procedure was used to model the distribution of sequential differences in surface interval duration, to allow for variation in dive characteristics between bouts (Mori et al. 2001). The log likelihood of all N_t absolute differences in surface interval duration t was expressed as a combination of fast (within bout) and slow (between bout) events (Luque and Guinet 2007):

$$log\ L_2 = \sum_{i=1}^{N_t} log[p\lambda_f e^{-\lambda_f\ \cdot\ t_i} + (1-p)\lambda_s e^{-\lambda_s\ \cdot\ t_i}] \tag{3.6}$$

where p is a mixing parameter representing the proportion of fast to slow process events in the sampled population; the subscripts $_f$ and $_s$ denote the fast and slow processes, respectively, and λ represents the probability of an event occurring in a given process per unit time (Sibly et al. 1990). A bout ending criterion (BEC), determining whether two successive dives should be grouped in the same bout or not can be calculated from Eq. (3.6):

$$BEC = \frac{1}{\lambda_f - \lambda_s} log \frac{p\lambda_f}{(1-p)\lambda_s} \qquad (3.7)$$

If the difference in surface interval duration between two successive dives exceeded the BEC, then they were grouped in different bouts.

nomenclature **BEC, Bout-ending criterion**

Statistical approach

BECs were determined for each individual separately, because foraging trip durations varied between them, and to avoid effects of interindividual variation in diving behaviour masking bout structure. The number of bouts, their duration, and the duration of intervals between bouts were thus calculated. Because both AFS and SFS dove almost exclusively during the night, the first two variables were divided by the number of night hours available during the foraging trip for each individual. Night time was defined as the number of hours between sunset and sunrise. Bouts consisting of a single dive were excluded from analyses because they were not deemed to be indicative of foraging behaviour.

AFS and SFS displayed a bimodal distribution of foraging trip duration (Luque et al. 2007*a*), with overnight (OFT, < 1 d) and long foraging trips (long foraging trip (LFT), > 1 d). Therefore, interspecific comparisons included fixed effects terms to test for differences between these types of foraging trip, and data for multiple trips of the same type were averaged for each individual, except for bout and post-bout duration because they represent variation within the foraging trip. A single value per individual and bout was considered for the latter two cases. A random effect term for individual was included, so mixed effects models (Pinheiro and Bates 2000) were used to describe data for the ith individual, jth species, and kth foraging trip type, as follows:

$$y_{ijk} = \beta_0 + \beta_j + \beta_k + \beta_{jk} + b_i + \epsilon_{ijk} \quad b_i \sim \mathcal{N}(0, \sigma_b^2), \epsilon_{ijk} \sim \mathcal{N}(0, \sigma^2) \tag{3.8}$$

where β_0 represents an intercept; $\beta_j, \beta_k, \beta_{jk}$ represent the fixed effects for species, foraging trip type, and corresponding interaction, respectively; b_i denotes the random effect for individual, and ϵ_{ijk} denotes an independent error term. The b_i and ϵ_{ijk} terms are assumed to be normally distributed, with mean zero, and variances σ_b^2 and σ^2, respectively. Multiple bout and post-bout duration for the same individual were, thus, included as part of ϵ_{ijk} for the corresponding models.

The significance of the interactions were assessed by comparing the models with and without the interaction term, using a log likelihood ratio test (Pinheiro and Bates 2000). The significance of other fixed effects was tested via Markov Chain Monte Carlo (MCMC) simulations based on samples of the posterior distribution of the model parameters (Baayen et al. 2008). All analyses were carried out in the GNU R system (R development Core Team 2007), with packages `diveMove` for dive behaviour analysis (Luque 2007) and `lmer` for fitting mixed effects models. Results are presented as means ± SE, unless stated otherwise. Although abbreviations for terms are introduced on first use, Appendix 1 shows the abbreviations used throughout the manuscript.

3.2.3 Results

Dive data from a total of 96 females were obtained, providing information from 277 foraging trips (Table 3.2). Most dives (83%) occurred in bouts for both species. However, this proportion was significantly ($\chi^2 = 1157$, *df* $= 1$, $P < 0.001$) larger in SFS (SFS = 86.4%, AFS = 78.8%), indicating that isolated dives were relatively more common in AFS. The number of bouts per night of foraging trip was larger in AFS (log-transformed to normalize residuals; $F_{1,148} = 58.85$, $P < 0.001$, Fig. 3.4a), regardless of foraging trip type (interaction term: $\chi^2 = 0.08$, $P = 0.78$). No significant differences between foraging trip types were found ($F_{1,148} = 0.07$, $P = 0.8$), and the pooled estimates for each species were 35.7 ± 1.05 and 21.5 ± 1.05 bouts per night for AFS and SFS, respectively. Examples of typical dive profiles are available in the supplementary Appendix 2.

The BEC was significantly higher for SFS during both seasons ($F_{1,88} = 52.39$, $P < 0.001$), and higher for both species during the 2001 season ($F_{1,88} = 7.42$, $P < 0.01$). Although this suggests that foraging conditions may have differed between seasons, data for both of them were pooled for further analyses because there was no interaction between species and season ($F_{1,88} = 1.55$, $P = 0.2$), and interannual differences were not the focus of this paper.

Dive bout structure

The total time spent in bouts per night was similar between species ($F_{1,144} = 2.00$, $P = 0.2$) and foraging trip types ($F_{1,144} = 0.01$, $P = 0.9$), without any interaction between both factors (interaction term $\chi^2 = 0.01$, $P = 0.92$, Fig. 3.4b). Pooled estimates for each species were 9.6 ± 1.05 and 10.6 ± 1.05 h per night for AFS and SFS, respectively. Bout duration, however, was significantly higher in SFS during both foraging trip types ($F_{1,9520} = 43.37$, $P < 0.001$, Fig. 3.4c); consistent with the higher number of bouts per night for AFS, but similar time spent in those bouts. Bout duration was similar between foraging trip types ($F_{1,9520} = 0.24, P > 0.9$), independently of the differences between species ($\chi^2 = 0.88$, $P = 0.35$).

The temporal distribution of foraging patches, as reflected by the density distribution post-bout durations, showed that AFS encountered patches at a slightly faster rate than SFS (Fig. 3.7). The difference was significant for OFTs (Kruskal-Wallis $\chi^2 = 4.60$, $df = 1$, $P = 0.03$) and LFTs ($\chi^2 = 91.68$, $df = 1$, $P < 0.001$), but small. Patch encounter rate, as measured by post-bout duration, did not differ significantly between foraging trip types ($\chi^2 = 2.62$, $df = 1$, $P = 0.11$). Foraging bout depths were most frequent near the surface for both species, but their relative frequencies were higher in AFS near the surface and below 80 m, while depths between 30 and 60 m were more heavily used by SFS females (Fig. 3.5).

Behavioural and physiological limits

The absolute number of meters that fur seals swam per unit time during the bottom phase of dives was significantly higher in SFS ($F_{1,149} = 13.2$, $P < 0.001$), independently of foraging trip type ($\chi^2 = 2.08$, $P = 0.15$). SFS swam 0.13 ± 0.006 m $\cdot$ s^{-1}, and AFS 0.10 ± 0.006 m $\cdot$ s^{-1} while at the bottom of dives. Furthermore, this rate appeared to be higher for both fur seal species during LFTs (0.12 ± 0.005 m $\cdot$ s^{-1}) than OFTs (0.10 ± 0.006 m $\cdot$ s^{-1}). This difference was significant ($F_{1,149} = 22.3$, $P < 0.001$).

The mean swim speed during the bottom phase of the dive did not differ between species ($F_{1,58} < 0.01, P > 0.9$), nor between foraging trip types ($F_{1,58} = 0.14, P = 0.7$), without interaction between these factors ($\chi^2 = 0.01$, $P = 0.9$). Similarly, mean swim speed during surface intervals did not differ between species for OFTs ($F_{1,20} = 1.18, P = 0.29$), nor for LFTs ($F_{1,36} = 4.1, P = 0.05$), despite a significant interaction between foraging trip type and species ($\chi^2 = 4.35, P = 0.04$)

The relationship between the duration of the briefest surface interval and dive duration showed no changes in surface interval for dives lasting up to almost 150 s in both species (Fig. 3.8). However, surface intervals following dives that were longer than this value increased steadily for AFS, whereas SFS showed a similar response for dives beyond 250 s in duration (Fig. 3.8), despite the larger rate of vertical movements they showed at the bottom of dives.

3.2.4 Discussion

We hypothesized that lactating female AFS have higher energy demands during lactation and, therefore, should spend greater effort foraging to meet those demands. Female AFS displayed higher indices of diving effort, reduced patch residence times, and briefer post-bout intervals, suggesting that they spent more effort foraging, and encountered prey patches at a faster rate. An important premise of our analyses is that both species forage optimally; specifically, that they maximize energy intake rate, relative to physiological constraints. Previous results have shown subtle interspecific differences in diet and dive depth associated with differences in life history and pup physiology (Luque et al. 2007*a*), so behavioural and physiological constraints may not be similar between AFS and SFS. Therefore, the optimal foraging behaviour (e.g. time spent in foraging patches and patch encounter rate) may also differ between species, and affect their rates of energy intake. Our results largely supported these predictions, and suggest a possible origin for the differences in foraging behaviour. We review the assumptions that were required to use our approach, and discuss the implications of our results for inferring the characteristics of the foraging habitat of sympatric AFS and SFS.

Assumptions

Using the information on differences in physiological constraints required making assumptions regarding the diving behaviour of fur seals (Mori et al. 2002, 2005, Mori and Boyd 2004*b*). A major assumption of the model is that energy intake is a function of time spent at the bottom of dives; i.e. prey is assumed to be obtained during the bottom phase of dives. Although it was not possible to ascertain whether this assumption was held with a two-dimensional dive profile and sampling interval of 5 s, direction reversals (wiggles) during descent or ascent phases were rare. Furthermore, the mean vertical distance covered during the bottom phase of dives (a measure of the amount of wiggling) was relatively high for both species (AFS = 12.7 m; SFS = 15.0 m) for dive depths > 10 m. These values exclude shallow V-shaped dives, which are indicative of travelling behaviour. Therefore, fur seals from La Mare aux Elephants probably concentrated their energy intake during bottom time.

A more fundamental assumption of the model is that fur seals dove optimally, so as to maximize the rate of energy intake during the dive cycle. Foragers may not always use an energy intake rate maximizing currency to behave optimally (Caraco 1980), as other factors play important roles in determining what behaviour is optimal under particular time scales. Nonacs (2001) reviewed a number of studies testing predictions based on this assumption and found a consistent bias in the predictions, arguing that inclusion of the forager's state (e.g. nutritional status and predation risk) in the models can improve the predictive power of the models. Heithaus and Frid (2003) proposed a model to account for predation risk during the surface interval for diving predators, which may help to explain why diving behaviour is often considered suboptimal, according to previously used models. Killer whales are common around Iles Crozet during the summer (Guinet 1992), but they feed mainly on penguins and elephant seals at this location. Although the risk of predation on fur seals can be high in some populations (Boveng et al. 1998), it is probably low at Ile de la Possession, because none of the females identified at La Mare aux Elephants were lost while they had a pup to nurse, nor were any visible wounds or scars detected, that could have been inflicted by a predator. Nonetheless, studies to determine whether there are differential effects of predation risk on the foraging behaviour of sympatric fur seals at Ile de la Possession may provide further insights into the mechanisms driving the observed differences.

Closely related to predation risk, the nutritional status of fur seals is another potential influence on the observed differences in foraging behaviour because animals may tradeoff energy gain against safety from predators (Nonacs 2001, Wirsing et al. 2008). Direct measurements of fat stores, the primary form of energy storage in pinnipeds, are not available for our study animals. However, a concurrent study showed that foraging trips at Ile de La Possession were among the briefest reported for each species at comparable stages of lactation (Luque et al. 2007*a*). Furthermore, the large proportion of overnight foraging trips, the relative proximity (50-100 km) of foraging grounds (Bailleul et al. 2005), and the relatively fast growth rates of pups compared to other populations of both species, suggest that neither of them was under nutritional stress. Differences in energy stores between species under such conditions are expected to have a small influence on foraging behaviour (Houston et al. 1993, Nonacs 2001).

Behavioural versus physiological differences

We found conflicting evidence regarding the level of activity of fur seals, measured as the mean speed and absolute number of meters that fur seals swam during the bottom phase of dives. The former showed no differences between fur seal species, but the latter showed higher activity levels in SFS females. Speed is typically measured by counting the number of revolutions per unit time taken by a turbine on TDRs, which are susceptible to clogging by debris (Shepard et al. 2008). Therefore, speed measurements for any given dive phase are not available with the same regularity as depth measurements, despite having been taken with the same sampling frequency. Consequently, fewer speed measurements were available for our comparisons of mean speed during any given dive phase, so the power of statistical comparisons was reduced relative to tests based on depth measurements. The vertical meters that fur seals swam per unit time during the bottom phase of dives may, thus, have been a better index of activity level, and our results suggest that SFS females were more active during this phase. Despite the behavioural difference during the bottom of dives, SFS females showed increasing surface intervals following longer dives than AFS females.

Our data suggest that an important physiological parameter, the aerobic dive limit (ADL), is higher in SFS than in AFS females. This result was unexpected and counter-intuitive because maximum dive depth was highest for AFS females, which were expected to be associated with a higher ADL. Lactating AFS females required exponentially longer periods at the surface when dive duration exceeded 150 s, while SFS females responded similarly, but to dives exceeding 250 s in duration. Consistent with these observations, SFS dove deeper and for longer periods of time, on average. ADL calculations based on direct measurements of oxygen stores and diving metabolic rates of fur seals from South Georgia (Costa et al. 2004) yielded a value (96 s) that is much lower than that reported here, especially considering the larger body mass of animals in that study. However, our data cannot easily be compared with direct measurements of ADL, and factors such as fur seals exceeding the ADL during deep diving bouts could account for the difference. Unfortunately, similar data are not available for SFS females, but if the tendency of study animals to exceed the ADL is similar, then the observed interspecific differences may parallel actual differences in ADL. Costa et al. (2004) suggest that the tendency of epipelagic feeders such as AFS and SFS to exceed the ADL are indeed expected to be similar and relatively low. Although direct measurements of diving metabolism are needed to corroborate it, the differences illustrated in Fig. 3.8 are likely a result of differences in actual ADL.

Inferring foraging patch characteristics

Previous analyses suggested that AFS and SFS females from La Mare aux Elephants used similar foraging areas during the 2001 and 2002 breeding seasons (Bailleul et al. 2005). Dietary analyses (Luque et al. 2007*a*), indicate that these fur seals also feed on the same myctophid fish species, albeit in different proportions (Luque et al. 2007*a*). Similar results have been found in sympatric populations at Macquarie Island (Robinson et al. 2002). The present study suggests that differences in physiological constraints may have led to different temporal and vertical distribution of diving, despite similarities in horizontal distribution of foraging locations and prey species. Whereas AFS foraged between the surface and 20 m more frequently than SFS females, the latter foraged more extensively between 30 and 60 m. Furthermore, both species reduced the frequency of foraging below 80 m, but SFS females did so more rapidly, and dive bouts below 140 m were only observed in AFS females. Assuming that dive bouts reflect foraging in different prey patches, AFS females exploited more patches per night of foraging, and a larger fraction of patches close to the surface. It may have been more profitable for AFS females to rapidly move between different patches at shallow depths, thereby reducing mean dive time and, possibly, the extent of anaerobic diving also (Costa et al. 2004).

Similar segregation of foraging depth has been observed in macaroni (*Eudyptes* *chrysolophus*) and gentoo (*Pygoscelis papua*) penguins at Bird Island, South Georgia (Mori and Boyd 2004*b*), showing some analogies in their response with the fur seals in this study. Macaroni penguins increased surface times in response to briefer dive durations (Mori and Boyd 2004*b*, Fig. 1), so their ADL is presumably lower than gentoo penguins. Macaroni penguins concentrated their foraging bouts at shallower depths compared to gentoo penguins, analogous to the higher frequencies of shallow bout depths observed in AFS compared to SFS females at La Mare aux Elephants. Although direct measurements of prey density and abundance at different depths were not available in the present study to validate an index of patch quality Mori and Boyd (IPQ; 2004*a*), it can be calculated with the available data to examine potential interspecific differences in foraging patch quality. According to Mori and Boyd (2004*a*), energy intake rate (G) can be expressed in terms of dive duration (u) and travel time from/to the surface (τ) as $G = a \times (u - \tau)^x/(u + y(u))$, where $y(u)$ is surface time, which is a function of dive duration, obtained from Fig. 3.8. If divers regulate dive duration so as to maximize the rate of energy intake, the IPQ for a dive can be determined by finding the value of x that maximizes G. The IPQ thus calculated indicates that foraging patch quality is higher for AFS below 50 m, suggesting that this species foraged more profitably deeper in the water column than SFS (Fig. 3.6). Concurrent measurements of the distribution and densities of different prey species and foraging behaviour of their air-breathing predators are needed to evaluate this suggestion. Since the IPQ may be similar between species at shallow depths, why did SFS females not exploit patches at these depths as extensively as AFS females, despite their higher ADL? Conversely, why did AFS females exploit deep patches more extensively than their congenerics, despite their lower ADL?

nomenclature **IPQ, Index of patch quality**

Optimal diving models (Mori 1998*a*,*b*) predict that divers with higher ADLs should find the optimal depth of foraging deeper in the water column, for any given prey patch quality. The models also predict that anaerobic diving is favourable when the prey patch is deep and of high quality (Mori 1998*b*). SFS females may thus require higher prey patch qualities near the surface to dive optimally. Factors such as swimming mechanics (Fish et al. 2003, Sato et al. 2007), and searching and/or travelling behaviour (Hindell et al. 2002) may explain why these favourable conditions were encountered less frequently by SFS compared to AFS females above 20 and below 80 m. For instance, young adult AFS and SFS show significant differences in fore- and hind-flipper size and shape (Bester and Wilkinson 1989, Luque et al. 2007*b*). Supporting this conjecture, AFS females showed a larger proportion of isolated dives, suggesting that they searched for foraging patches more extensively. Interestingly, activity during the bottom foraging phase of dives was higher in SFS, but their behavioural ADL was higher, suggesting that differences in the relationship between surface interval and dive duration were a result of physiological, rather than behavioural, constraints. Otherwise, the behavioural ADL would have been lower in SFS. Further studies comparing foraging efficiency between these species should help explain this pattern.

Indeed, the briefer bout durations and post-bout intervals, in addition to the larger proportion of exploratory dives, observed in AFS females may allow them to sample prey patches near the surface more frequently, thus foraging with better knowledge of conditions in this part of the habitat (Charnov 1976). Dive traces from AFS females at La Mare aux Elephants display stronger diel changes in dive depth than SFS females (see examples in accompanying electronic supplementary material), indicating that they find their deepest foraging patches during the crepuscular vertical migration of their myctophid prey (Boyd et al. 1994, McCafferty et al. 1998, Luque et al. 2007*a*). Some myctophid fish species of this sector of the Southern Ocean are known to form denser patches at their deep daytime depth locations than during the night (Bost et al. 2002), when they are patchily distributed near the surface. AFS, and to a much lesser extent SFS, females may profit from the more densely aggregated fish during dawn and dusk, as they shift between these depth locations and spatial organizations. Our observations, therefore, suggest that AFS females spent a larger fraction of foraging time in patches of higher quality, particularly after dusk and before dawn, both during OFTs and LFTs, even when costs may have been higher due to deep (Luque et al. 2007*a*), anaerobic diving.

To conclude, we have shown interspecific differences in the temporal distribution of diving and foraging depth between sympatric AFS and SFS, which are consistent with the hypothesis that lactation pressure is higher in AFS. The larger number of bouts, briefer post-bout interval, and higher propensity to dive anaerobically in AFS, suggest that they spent more effort foraging. Furthermore, they appeared to concentrate that effort in prey patches of higher quality. These differences were associated with lower ADL, briefer duration of lactation, and higher pup energy demands in AFS. Gentry et al. (1986) hypothesized that a suite of fur seal life history traits, including foraging behaviour and lactation duration, follow a latitudinal gradient, ultimately determined by environmental seasonality and predictability. Since then, additional information from species inhabiting temperate latitudes has indicated that prey ecology may be more important than latitude, as a factor influencing foraging and maternal behaviours (Francis et al. 1998). Moreover, our results suggest that intrinsic differences in physiological constraints and lactational demands play important roles in determining the fine scale foraging behaviour in sympatric populations of some species, despite similarities in diet and prey ecology.

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Table 3.2. Summary of dive data obtained from lactating female Antarctic (AFS) and subantarctic (SFS) fur seals fitted with time-depth recorders (TDRs) on Ile de la Possession, in the breeding seasons of 2001-02 and 2002-03

Species	Breeding Season	Body mass (kg)	*N*	Foraging trips	Dives	BEC[a] (s)	Bouts	Dives in Bouts	Mean dive depth (m)	Mean dive duration (s)
AFS	2001	33.2 ± 0.44	37	102	42095	54.9 ± 0.44	3814	33522	31.2 ± 0.32	80.1 ± 0.60
	2002	31.6 ± 0.58	12	30	17541	38.5 ± 0.83	1614	13500	22.8 ± 0.70	73.4 ± 1.32
	Both	32.7 ± 0.36	49	132	59636	50.9 ± 0.33	5428	47022	29.2 ± 0.24	78.5 ± 0.42
SFS	2001	30.6 ± 0.55	37	113	39102	84.8 ± 0.91	2839	33780	42.1 ± 0.44	94.2 ± 0.63
	2002	30.4 ± 0.78	10	32	17693	72.8 ± 1.44	1156	15302	32.9 ± 0.70	90.2 ± 1.68
	Both	30.5 ± 0.45	47	145	56795	81.7 ± 0.61	3995	49082	39.7 ± 0.31	93.2 ± 0.46

[a] Bout ending criterion

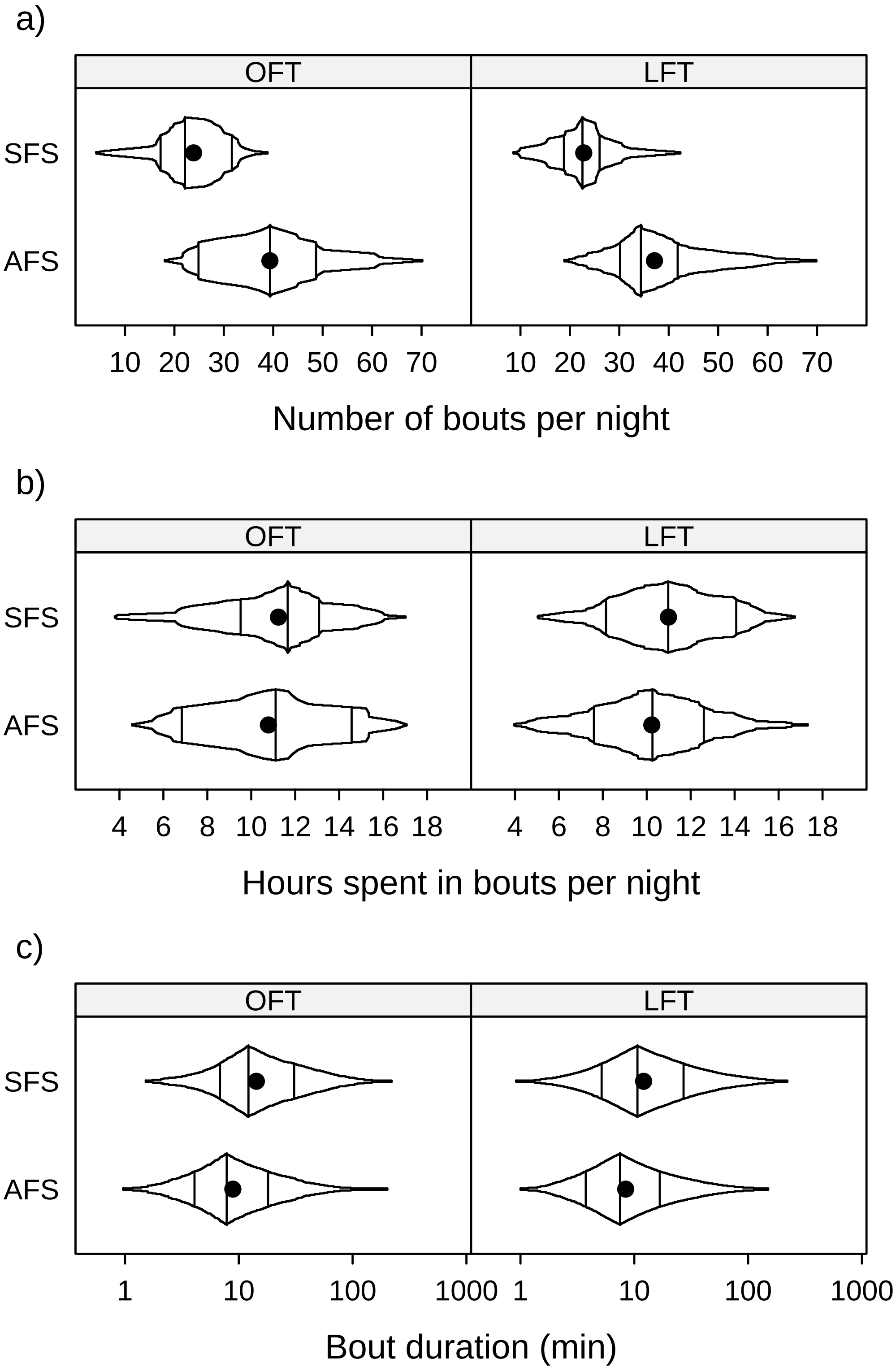

Figure 3.4. Lactating Antarctic fur seal (AFS) females perform more bouts per night, spend a similar amount of time in bouts per night, and their bouts are briefer than in lactating subantarctic fur seal (SFS) females on Ile de la Possession

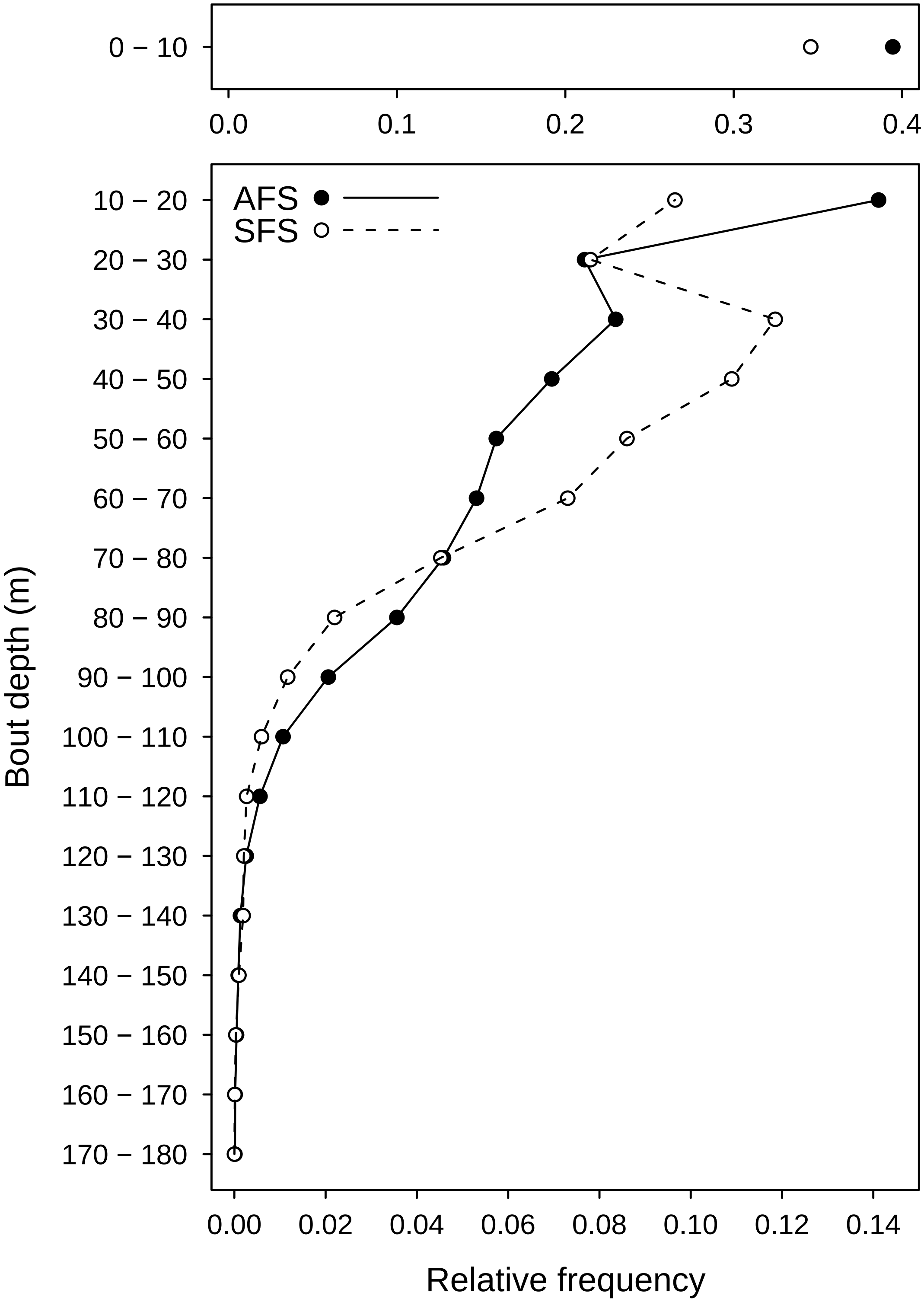

Figure 3.5. Lactating Antarctic (AFS) fur seal females forage more frequently than subantarctic (SFS) females between the surface and 20 m, and below 80 m. SFS females spend a greater proportion of their bouts between 30 and 60 m

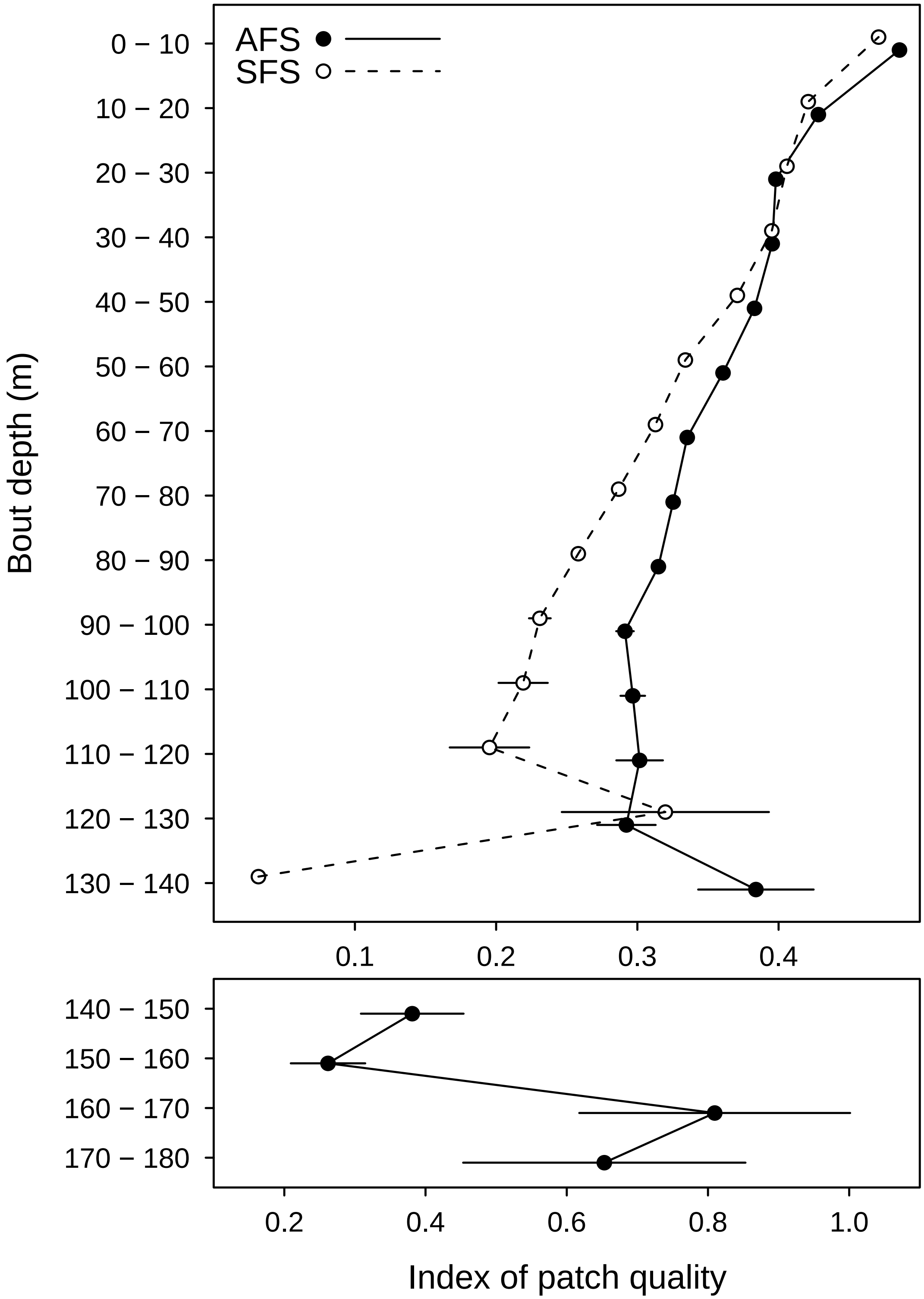

Figure 3.6. Lactating Antarctic (AFS) fur seal females encounter foraging patches with higher index of patch quality (IPQ) than subantarctic (SFS) fur seal females at depths between 50 and 100 m. They also exploit patches at depths > 140 m, which are not used by SFS and where variation in IPQ is large. Values are mean ± SE

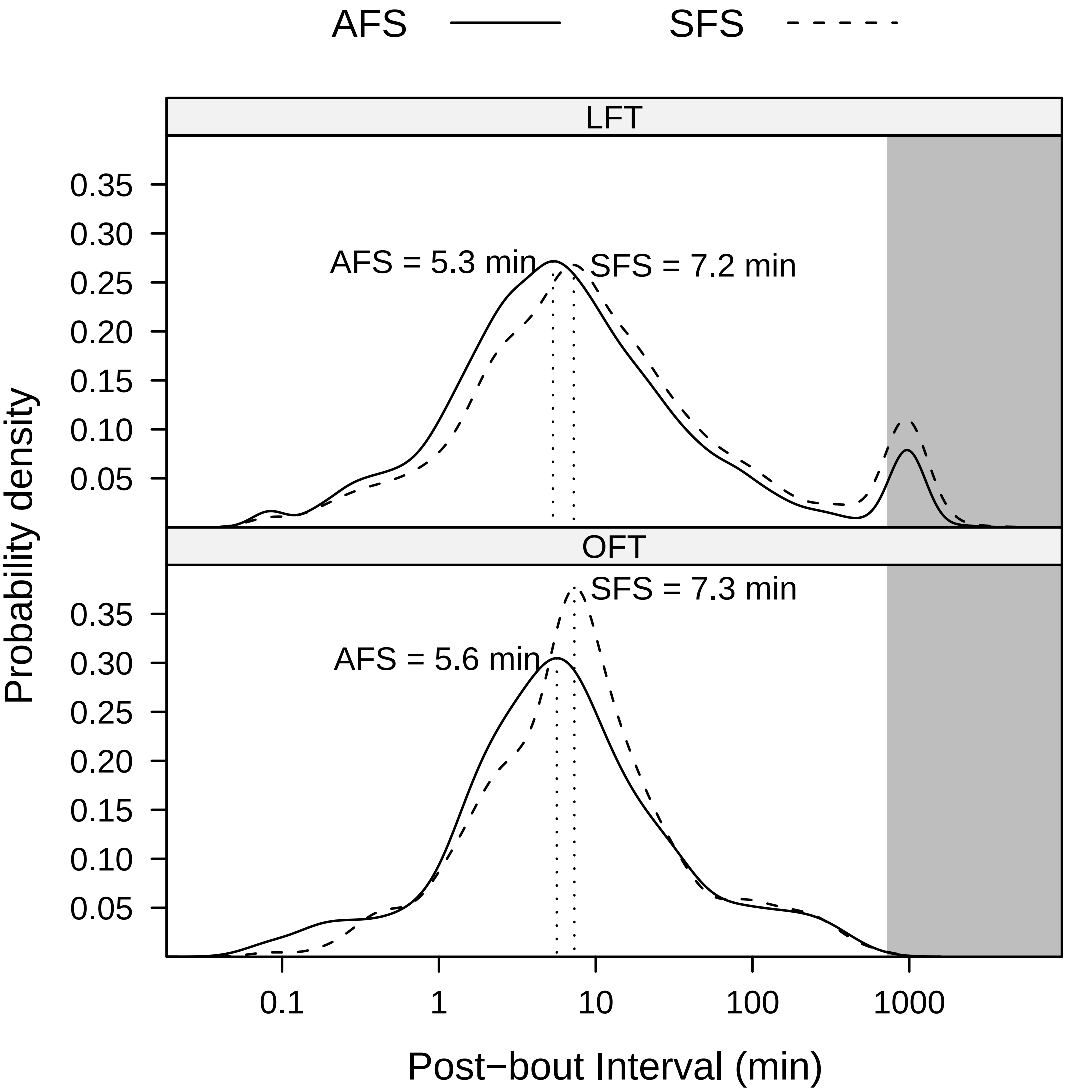

Figure 3.7. The temporal separation between foraging patches, as indicated by post-bout intervals, is briefer in lactating Antarctic (AFS) than subantarctic fur seal (SFS) females, during long (LFT) and overnight (OFT) foraging trips. The dotted lines indicate the post-bout interval with the highest kernel density estimate. The shaded region denotes intervals > 12 hr; i.e. bouts occurring on different foraging nights

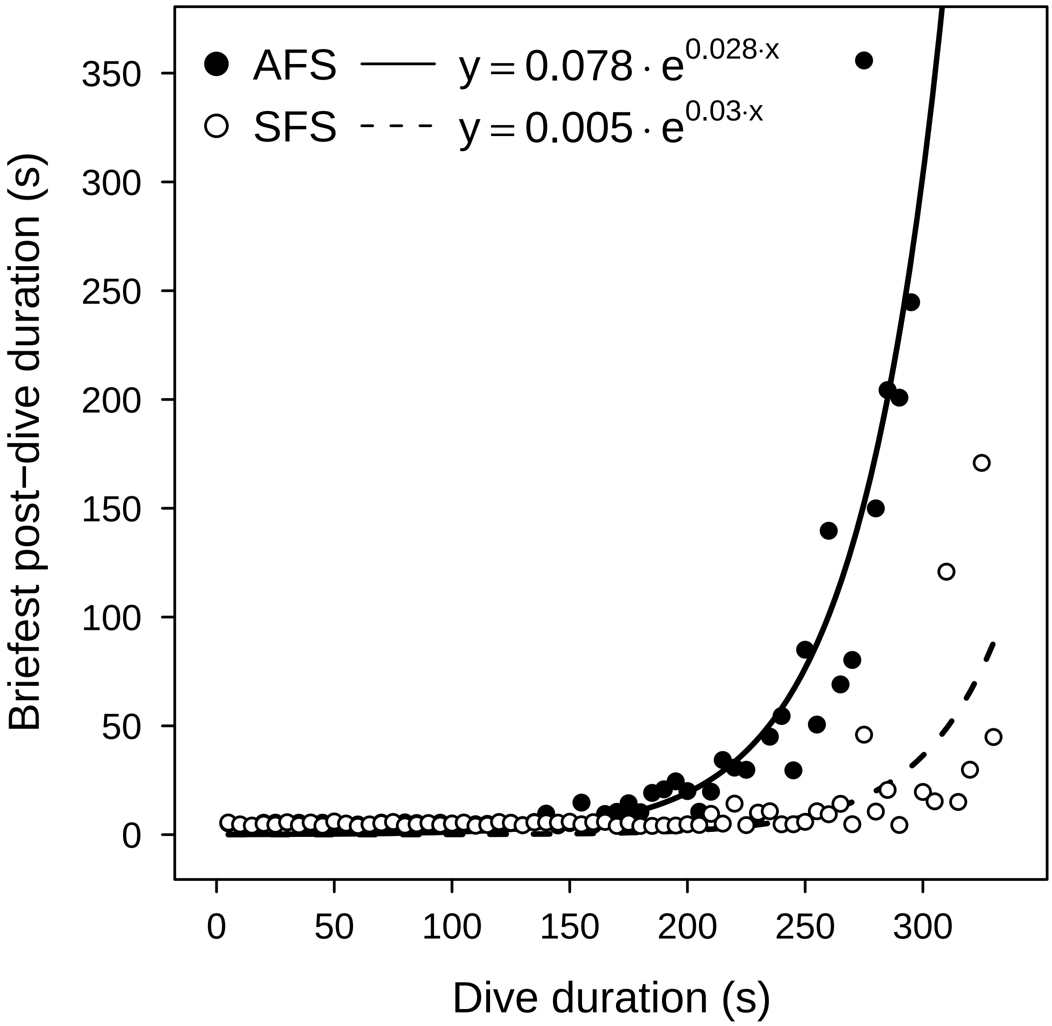

Figure 3.8. Briefest surface post-dive intervals increase exponentially for dive durations longer than 150 and 250 s in lactating Antarctic (AFS) and subantarctic (SFS) fur seal females, respectively

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Temporal structure of diving behaviour in sympatric Antarctic and subantarctic fur seals

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ABSTRACT: Lactation is considerably briefer (4 vs. 10 mo) and daily pup energy expenditure higher in Antarctic (AFS) than in subantarctic fur seals (SFS), even in sympatric populations of both species, where their foraging locations and diets are similar. Therefore, lactational demands may be higher for AFS females. We investigated whether sympatric lactating AFS and SFS females differ in their physiological or behavioural diving capacities, and in the temporal structure of foraging behaviour. Mean dive depth and duration were greater in SFS, but dives below 140 m were performed only by AFS. An index of activity level during the bottom phase of dives, when fur seals are thought to capture prey, was higher in SFS. Despite these differences, SFS females showed a steady increase in the minimum postdive interval following dives lasting longer than 250 s, compared to the steady increase following dives lasting longer than only 150 s in AFS. These results suggest that physiological constraints on diving behaviour are stronger on AFS females, and that the behavioural aerobic dive limit is greater for SFS. Assuming that dive bouts reflect foraging in prey patches, AFS females exploited more patches per unit time, and remained in them for briefer periods of time, compared to SFS females. Dive bout structure did not differ between overnight and long foraging trips. Our data suggest that AFS females spend greater foraging effort, but may gain access to prey patches of better quality, which may help them cope with higher lactational demands.

KEY WORDS: Optimal foraging · Foraging niche segregation · Foraging behaviour · Diel trends · Diurnal activity · Myctophidae · Syntopy · Archival tags

INTRODUCTION

Exploitative competition for food between animals is difficult to assess, partly because it requires knowledge of whether the level of their common resources is limiting or not (Birch 1957, MacArthur & Levins 1964). Yet it is considered a major component of species interactions, and influences community structure (Milinski & Parker 1991). In the absence of data on the level of common resources, exploitative competition is often inferred from measurements of resource overlap or manipulations of population densities (Schoener 1974). However, an approach based on comparisons of the biology and behaviour of potentially competing species may be more useful for understanding interspecific interactions (Tilman 1987). This approach has been used to study mechanisms of coexistence in a broad range of species (Stamps 1983, Cowlishaw 1999, Hull 1999, Robinson et al. 2002).

Using this approach, Ballance et al. (1997) showed that competitive ability and energetic constraints play a major role in the structure of seabird assemblages. Sympatry or syntopy in morphologically similar, related species is particularly attractive for studying these interactions. Under such conditions, it is possible to compare the ecology of co-occurring species, while minimizing the influence of extraneous factors, which are difficult or impossible to control. Studies of related seabirds have provided evidence of physiological constraints on the behavioural response of coexisting

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predators to heterogeneity in the distribution of common prey resources (Hull 1999, Mori & Boyd 2004b). Therefore, studies such as these can be used as a basis for predicting the outcome of reductions in prey abundance and/or availability.

Lactation constrains the foraging behaviour of mammals (Sæther & Gordon 1994), especially in the marine environment (Costa & Williams 1999). Therefore, new insights into the mechanisms linking prey distribution and predator behaviour can be gained by comparing the foraging behaviour of sympatric marine mammals. Otariid (fur seals and sea lions) pinnipeds are good models in comparative foraging ecology because they exhibit large variation in adult body size and lactation duration, while other life history traits are relatively homogeneous (Ridgway & Harrison 1981). Female body mass varies from ~30 (in Galápagos fur seals *Arctocephalus galapagoensis* [Heller 1904]) to 275 kg (in Steller sea lions *Eumetopias jubatus* [Schreber 1776]), and lactation duration varies from 4 (in Antarctic fur seal *Arctocephalus gazella* [Peters 1875]) to 36 mo (in Galápagos fur seals; range 12 to 36 mo; Trillmich & Kooyman 1986). Large pinnipeds have higher aerobic dive limits (ADL) than smaller ones (Kooyman 1989), so they can dive for longer periods of time (Halsey et al. 2006) without the negative effects of increased lactic acid concentration. Consequently, they have more time available for prey search and capture. However, species of similar body mass can display large differences in lactation duration, energy transfer to pups, and patterns of energy allocation by pups (Arnould 1997, Arnould et al. 2003). Therefore, the interplay among body mass, foraging behaviour, and lactation duration remain unclear. Sympatric otariids of similar body mass, yet different lactation duration, offer a unique opportunity to understand the physiological and behavioural tradeoffs faced by breeding females during lactation.

Diving marine predators often dive in bouts, i.e. most dives occur in rapid succession, while the rest are separated by longer intervals, and each bout may indicate foraging in a particular patch (Mori & Boyd 2004a). Researchers thus deduced that the temporal structure of diving may be used to infer the distribution and characteristics of foraging patches in several seabirds (Kato et al. 2000, Mehlum et al. 2001), and pinnipeds (Mori & Boyd 2004a, Mori et al. 2005). This provides a framework for comparing the foraging behaviour of sympatric marine mammals in relation to a common prey resource.

Antarctic and subantarctic (*A. tropicalis* [Gray 1872]) fur seals (AFS and SFS, respectively, hereafter) have broadly different spatial distributions. AFS breed mostly south of the Antarctic Polar Front, while SFS do so mostly north of it, but they breed sympatrically at 3 locations (Bonner 1999): Macquarie Island, Ile de la Possession (Iles Crozet), and Marion Island (Prince Edward Islands). Adult females of these species have similar body mass and show little differences in at-sea distribution and diet when sympatric (Klages & Bester 1998, Robinson et al. 2002, Bailleul et al. 2005, Luque et al. 2007a), yet wean pups at 4 in (AFS) vs. 10 mo of age in (SFS) (Bester & Bartlett 1990), as they do in allopatric populations. Furthermore, AFS pups show higher daily energy expenditures (Arnould et al. 2003), and grow in body length faster (Luque et al. 2007b) at Ile de la Possession. Thus, their mothers must meet these demands in addition to their own, and also complete lactation in <½ the time compared to SFS. Lactational demands may thus be higher in AFS, which females should satisfy during their foraging trips to sea.

Previous comparisons of diving behaviour between these species in sympatry have not shown major differences at the scale of entire foraging trips (Goldsworthy et al. 1997, Robinson et al. 2002). At Ile de la Possession, however, overnight foraging trips (OFTs) are significantly more frequent in SFS, and AFS appear to spend a greater proportion of their time at sea (Bester & Bartlett 1990, Bailleul et al. 2005, Luque et al. 2007a), as in Marion Island. Differences at finer scales have been studied at Ile de la Possession, where lactating female AFS exhibit stronger diel variation in dive depth, with relatively shallow diving (AFS: 25 to 30 m; SFS: 35 to 50 m) during the noncrepuscular hours of the night, and deep diving (AFS: 45 to 65 m; SFS: 40 to 50 m) during crepuscular hours (Luque et al. 2007a). At Marion (Klages & Bester 1998, Ferreira & Bester 1999) and Macquarie Islands (Robinson et al. 2002), no interspecific differences in diet were found. Scat analyses suggest that sympatric AFS and SFS feed on the same prey species (myctophid fish), although differences in their relative abundance were found at Ile de la Possession (Luque et al. 2007a). Comparisons of the temporal structure of diving behaviour between AFS and SFS, however, are unavailable, but may help us understand how these species with different lactational demands respond to distribution of similar prey.

Diving capacity of otariid species with similar body mass is expected to be similar (Kooyman 1989), assuming other factors do not differ. In this case, optimal diving models predict similar optimal foraging depth (Mori 1998a, 2002). Optimal diving models typically assume that divers maximize energy intake rate, although predation risk may significantly influence such predictions (Frid et al. 2007). They also predict that divers should increase the time spent in foraging patches as depth increases (Mori 1998b, Thompson & Fedak 2001), but only if diving remains aerobic (Houston & Carbone 1992) or patch quality (as reflected by prey density) increases. A previous study does not support the first prediction of similar optimal foraging depth (Luque et al. 2007a), suggesting that important physiological or behavioural differences exist between female AFS and SFS, which may affect their exploitation of prey patches. Therefore, we investigated whether the temporal structure of diving behaviour and vertical distribution of foraging patches differ between fur seal species at Ile de la Possession. Given the briefer lactation and higher daily energy requirements of AFS pups, we tested the hypothesis that female AFS have higher energy demands during lactation, and should spend more foraging effort, despite their overlapping foraging areas.

MATERIALS AND METHODS

Data on diving behaviour of AFS and SFS was obtained at La Mare aux Elephants (46° 22′ 29″ S, 51° 40′ 13″ E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001–02 (4 December to 25 March) and 2002–03 (1 December to 16 March) breeding seasons (2001 and 2002 hereafter). A total of 277 (AFS: 153, SFS: 124) pups were individually marked as previously described (Georges & Guinet 2000, Arnould et al. 2003, Bailleul et al. 2005), providing a means to identify their mothers, a subset of which were equipped with time and depth recorders (TDRs; Table 1).

Diving behaviour. Animal capture and handling procedures are described in Luque et al. (2007a). Briefly, lactating females of each species were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different time-depth recorder (TDR) models (MK5, MK7, and MK8; Wildlife Computers) was glued to the dorsal fur between the scapulae, using a 2-component epoxy glue (AW 2101 Ciba Specialty Chemicals). Fur seals travelled 50 to 100 km from the colony to forage, and there were no significant differences in foraging trip duration, dive depth, or dive duration between individuals instrumented with different TDR models ($p > 0.5$ in all cases). Thus, data from the 3 models were pooled for interspecific comparisons. TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. MK8 TDRs also recorded speed to the nearest 0.02 m s^{-1}. Instruments were left on the seals for 1 to 11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals' return to the colony.

TDR data were downloaded to a portable computer, and analyses of the resulting time series of dive data were performed using custom written software package diveMove (Luque 2007), available through GNU R (R Development Core Team 2007). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e. continuous depth readings) was available for at least 6 h. This limit was selected to exclude brief excursions to sea for activities other than foraging, which occurred mostly during daytime, and contained isolated shallow dives (<20 m), in contrast to the bout-organized dives typical of foraging trips (Luque et al. 2007a).

Dives were defined as departures from the surface to depths ≥4 m plus the ensuing return to the surface. Dives to lower depths were not considered, as they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the instrument (Beck et al. 2000). Each dive was divided into descent, bottom, and ascent phases, where: (1) descent started at the surface and ended when no further increases in depth were detected; (2) ascent was defined from the end of the dive and, with the reversed time series, ending when no further increases in depth were detected; and (3) the bottom phase was the period between descent and ascent. Dives were thus described by their

Table 1. *Arctocephalus gazella* (AFS), *A. tropicalis* (SFS). Summary of dive data obtained from lactating females fitted with time-depth recorders (TDRs) on Ile de la Possession, in the breeding seasons of 2001–02 and 2002–03; BEC = bout-ending criterion. Data are either number or mean ± SE

Species	Breeding season	Body mass (kg)	N	Foraging trips	Dives	BEC (s)	Bouts	Dives in bouts	Mean dive depth (m)	Mean dive duration (s)
AFS	2001	33.2 ± 0.44	37	102	42095	54.9 ± 0.44	3814	33522	31.2 ± 0.32	80.1 ± 0.60
	2002	31.6 ± 0.58	12	30	17541	38.5 ± 0.83	1614	13500	22.8 ± 0.70	73.4 ± 1.32
	Both	32.7 ± 0.36	49	132	59636	50.9 ± 0.33	5428	47022	29.2 ± 0.24	78.5 ± 0.42
SFS	2001	30.6 ± 0.55	37	113	39102	84.8 ± 0.91	2839	33780	42.1 ± 0.44	94.2 ± 0.63
	2002	30.4 ± 0.78	10	32	17693	72.8 ± 1.44	1156	15302	32.9 ± 0.70	90.2 ± 1.68
	Both	30.5 ± 0.45	47	145	56795	81.7 ± 0.61	3995	49082	39.7 ± 0.31	93.2 ± 0.46

duration, maximum depth, bottom time, and postdive duration.

Fur seals catch their prey predominantly during the bottom phase of dives, although this has been demonstrated only for AFS (Hooker et al. 2002). As a measure of the level of activity during the bottom (foraging) phase of dives, we thus divided the absolute number of vertical meters each individual swam during this phase by bottom time. We also calculated mean swimming speed during the bottom phase of dives from fur seals deployed with MK8 TDRs. Speed measurements, however, do not correspond to true speed because they need to be calibrated against the true speed of the seals. Nonetheless, we used measured speed because we were more interested in comparing the levels of activity during the bottom phase of dives between species, rather than estimating true speed.

To investigate whether physiological constraints differ between species, we studied the relationship between the briefest postdive duration and dive duration binned at 5 s intervals. The dive duration beyond which the briefest postdive interval begins to rise was taken as a behavioural proxy for the ADL, i.e. the dive duration beyond which blood lactate levels rise, as a result of increasing anaerobic metabolism (Kooyman 1989).

Identification of dive bouts. Identification of bouts of most behaviours has traditionally relied on log-survivorship or log-frequency analysis (Gentry & Kooyman 1986, Sibly et al. 1990). However, Langton et al. (1995) pointed out that these methods include some level of subjectivity. The procedure involves fitting a curve to histogram data, an arbitrary choice of histogram class width, and adjustment for empty class intervals. Langton et al. (1995) presented an improved approach, based on maximum likelihood estimation, which uses the entire dataset to describe the frequency distribution of events such as diving. This procedure was used to model the distribution of sequential differences in surface interval duration, allowing for variation in dive characteristics between bouts (Mori et al. 2001). The log likelihood ($\log L_2$) of all N_t absolute differences in surface interval duration t is a combination of fast (within bouts) and slow (between bouts) events (Luque & Guinet 2007):

$$\log L_2 = \sum_{i=1}^{N_t} \log\left[p\lambda_\mathrm{f} \mathrm{e}^{-\lambda_\mathrm{f} t_\mathrm{i}} + (1-p)\lambda_\mathrm{s} \mathrm{e}^{-\lambda_\mathrm{s} t_\mathrm{i}}\right] \qquad (1)$$

where p is a mixing parameter representing the proportion of fast to slow process events in the sampled population; the subscripts f and s denote the fast and slow processes, respectively, and λ represents the probability of an event occurring in a given process per unit time t (Sibly et al. 1990). A bout ending criterion (BEC), determining whether two successive dives should be grouped in the same bout or not, can be calculated from Eq. (1) as:

$$\mathrm{BEC} = \frac{1}{\lambda_\mathrm{f} - \lambda_\mathrm{s}} \log \frac{p\lambda_\mathrm{f}}{(1-p)\lambda_\mathrm{s}} \qquad (2)$$

If the difference in surface interval duration between two successive dives exceeded the BEC, then they were grouped in different bouts.

Statistical approach. BECs were separately determined for each individual due to individual differences in foraging trip durations, and to avoid masking of bout structure by individual differences in diving behaviour. The number of bouts, their duration, and the duration of intervals between bouts were also similarly calculated. Because both AFS and SFS dived almost exclusively at night, the first two variables were divided by the number of night hours available during the foraging trip of each individual. Night time was defined as the number of hours between sunset and sunrise. Bouts consisting of a single dive were not deemed to indicate foraging behaviour, and were thus excluded from analyses.

Both AFS and SFS displayed bimodal distributions of foraging trip duration (Luque et al. 2007a), with overnight (OFT, <1 d) and long foraging trips (LFT, >1 d). Therefore, interspecific comparisons included fixed effects terms to test for differences between these types of foraging trip. Data for multiple trips of the same type were averaged for each individual, except for bout and postbout duration, which represent variation within the foraging trip. A single value per individual and bout was considered for bout and postbout duration. A random effect term for individuals was included, so mixed effects models (Pinheiro & Bates 2000) were used to describe data for the *i*th individual, *j*th species, and *k*th foraging trip type, as follows:

$$\begin{gathered} y_{ijk} = \beta_0 + \beta_j + \beta_k + \beta_{jk} + b_i + \varepsilon_{ijk} \\ b_i \sim \mathcal{N}(0, \sigma_b^2),\, \varepsilon_{ijk} \sim \mathcal{N}(0, \sigma^2) \end{gathered} \qquad (3)$$

where β_0 represents an intercept; $\beta_j, \beta_k, \beta_{jk}$ represent the fixed effects for species, foraging trip type, and corresponding interaction, respectively; b_i denotes the random effect for individual, and ε_{ijk} denotes an independent error term. The b_i and ε_{ijk} terms are assumed to be normally distributed, with mean zero, and variances σ_b^2 and σ^2, respectively. Multiple bout and postbout durations for the same individual were, thus, included as part of ε_{ijk} for the corresponding models.

The significance of the interactions was assessed by comparing the models with and without the interaction term, using a log likelihood ratio test (Pinheiro & Bates 2000). The significance of other fixed effects was tested via Markov Chain Monte Carlo (MCMC) simulations based on samples of the posterior distribution of the model parameters (Baayen et al. 2008). All analyses were carried out in the GNU R system (R Development Core Team 2007), with packages diveMove for dive behaviour analysis (Luque 2007) and lme 4 for fitting mixed effects models (Bates et al. 2008). Results are presented as means ± SE, unless stated otherwise.

RESULTS

Dive data from a total of 96 females were obtained, providing information from 277 foraging trips (Table 1). Most dives (83 %) occurred in bouts for both species. However, this proportion was significantly larger ($\chi^2 = 1157$, df = 1, $p < 0.001$) in SFS (86.4 vs. 78.8 %), indicating that isolated dives were relatively more common in AFS. The number of bouts per night of foraging trip was larger in AFS (log-transformed to normalize residuals; $F_{1,148} = 58.85$, $p < 0.001$) (Fig. 1a), regardless of foraging trip type (interaction term: $\chi^2 = 0.08$, $p = 0.78$). No significant differences between foraging trip types were found ($F_{1,148} = 0.07$, $p = 0.8$), and the pooled estimates for each species were 35.7 ± 1.05 and 21.5 ± 1.05 bouts per night for AFS and SFS, respectively. Typical dive profiles are shown in Appendix 1 www.int-res.com/articles/suppl/m372p277_app.pdf.

The BEC was significantly higher for SFS during both seasons ($F_{1,88} = 52.39$, $p < 0.001$), and higher for both species during the 2001 season ($F_{1,88} = 7.42$, $p < 0.01$). Although this suggests that foraging conditions may have differed between seasons, data for both seasons were pooled for further analyses because there was no interaction between species and season ($F_{1,88} = 1.55$, $p = 0.2$), and interannual differences were not the focus of this paper.

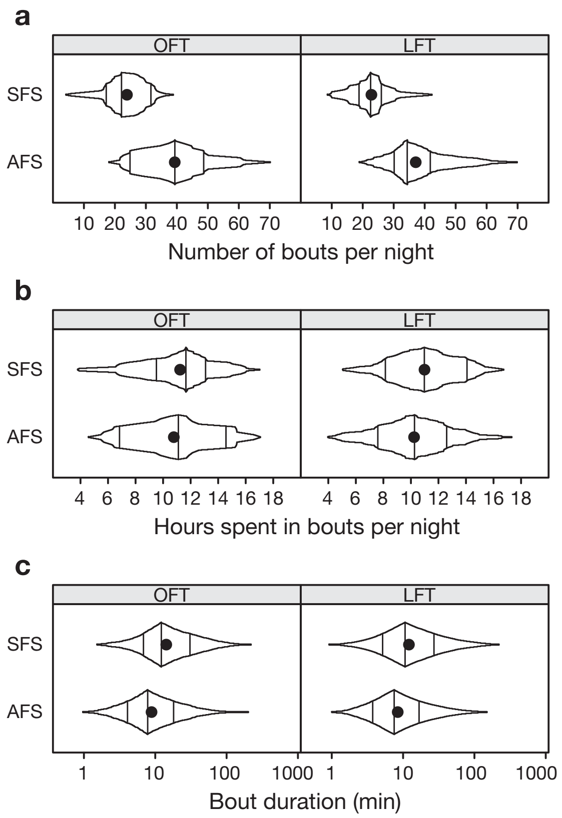

Fig. 1. *Arctocephalus gazella* (AFS), *A. tropicalis* (SFS). OFT: overnight foraging trips; LFT: long foraging trips. Lactating AFS females perform more bouts per night, spend a similar amount of time in bouts per night, and have briefer bouts than lactating SFS females

Dive bout structure

The total time spent in bouts per night was similar between species ($F_{1,144} = 2.00$, $p = 0.2$) and foraging trip types ($F_{1,144} = 0.01$, $p = 0.9$), without any interaction between both factors (interaction term $\chi^2 = 0.01$, $p = 0.92$) (Fig. 1b). Pooled estimates for each species were 9.6 ± 1.05 and 10.6 ± 1.05 h night^{-1} for AFS and SFS, respectively. Bout duration, however, was significantly longer in SFS during both foraging trip types ($F_{1,9520} = 43.37$, $p < 0.001$) (Fig. 1c) consistent with the higher number of bouts per night for AFS, but similar time spent in those bouts. Bout duration was similar between foraging trip types ($F_{1,9520} = 0.24$, $p > 0.9$), independently of differences between species ($\chi^2 = 0.88$, $p = 0.35$).

The temporal distribution of foraging patches, as reflected by the density distribution of postbout durations, showed that AFS encountered patches at a slightly faster rate than SFS (Fig. 2). Albeit small, the difference was significant for OFTs (Kruskal-Wallis $\chi^2 = 4.60$, df = 1, $p = 0.03$) and LFTs ($\chi^2 = 91.68$, df = 1, $p < 0.001$). Patch encounter rate, as measured by postbout duration, did not differ significantly between foraging trip types ($\chi^2 = 2.62$, df = 1, $p = 0.11$). Foraging bouts were most frequent near the surface for both species, but their relative frequencies were higher near the surface and below 80 m in AFS, while depths between 30 and 60 m were more heavily used by SFS females (Fig. 3).

Behavioural and physiological limits

The absolute number of meters that fur seals swam per unit time during the bottom phase of dives was significantly higher in SFS ($F_{1,149} = 13.2$, $p < 0.001$), and

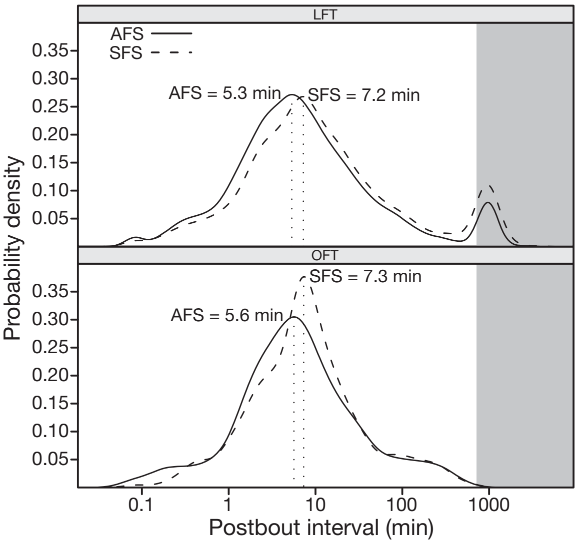

Fig. 2. *Arctocephalus gazella* (AFS), *A. tropicalis* (SFS). Kernel density estimates of postbout intervals during overnight foraging trips (OFT) and long foraging trips (LFT). The temporal separation between foraging patches, as indicated by postbout intervals, is briefer in lactating Antarctic (AFS) than in subantarctic fur seal (SFS) females, during both LFT and OFT. Dotted lines indicate the postbout interval with the highest kernel density estimate. Shaded regions denote intervals >12 h, i.e. bouts occurring on different foraging nights

was independent of foraging trip type (χ^2 = 2.08, p = 0.15). SFS swam 0.13 ± 0.006 m s^{-1}, and AFS 0.10 ± 0.006 m s^{-1} while at the bottom of dives. Furthermore, this rate was significantly higher ($F_{1,149}$ = 22.3, $p < 0.001$) during LFTs (0.12 ± 0.005 m s^{-1}) than during OFTs (0.10 ± 0.006 m s^{-1}) for both fur seal species.

The mean swimming speed during the bottom phase of dives did not differ between species ($F_{1,58} < 0.01$, $p > 0.9$), nor between foraging trip types ($F_{1,58}$ = 0.14, p = 0.7), and no interaction between these factors (χ^2 = 0.01, p = 0.9) was noted. Similarly, mean swimming speed during surface intervals did not differ between species for OFTs ($F_{1,20}$ = 1.18, p = 0.29), nor for LFTs ($F_{1,36}$ = 4.1, p = 0.05), despite a significant interaction between foraging trip type and species (χ^2 = 4.35, p = 0.04)

The relationship between the duration of the briefest surface interval and dive duration showed no changes in surface interval for dives lasting up to almost 150 s in both species (Fig. 4). However, surface intervals following dives longer than 150 s increased steadily for AFS, whereas SFS showed a similar response only for dives longer than 250 s (Fig. 4), despite the latter's larger rate of vertical movements at the bottom of dives.

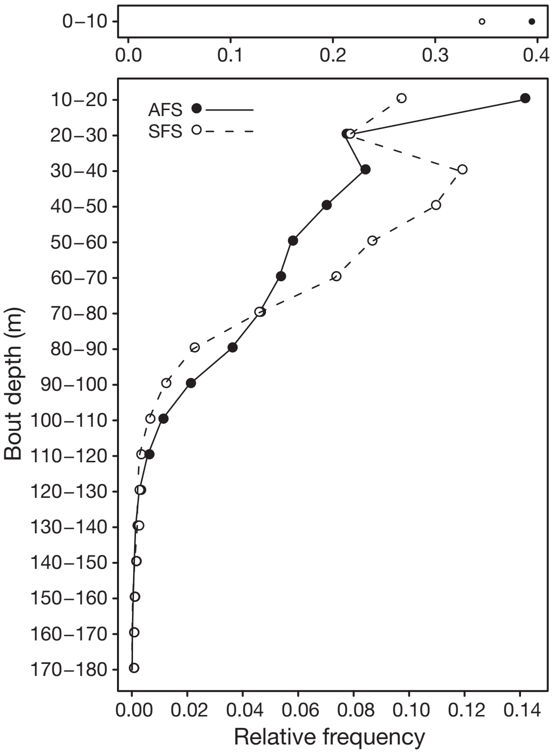

Fig. 3. *Arctocephalus gazella* (AFS), *A. tropicalis* (SFS). Lactating Antarctic fur seal (AFS) females forage more frequently than subantarctic (SFS) females between the surface and 20 m, and below 80 m. SFS females spend a greater proportion of their bouts between 30 and 60 m

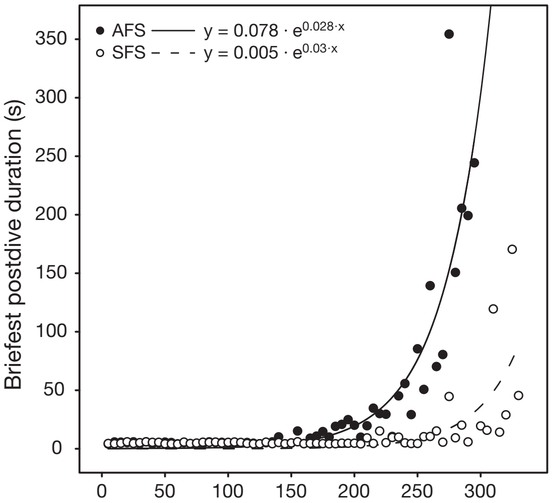

Fig. 4. *Arctocephalus gazella* (AFS), *A. tropicalis* (SFS). Briefest surface postdive intervals increase exponentially for dive durations longer than 150 and 250 s in lactating Antarctic (AFS) and subantarctic fur seal (SFS) females, respectively

DISCUSSION

We hypothesized that lactating female AFS have higher energy demands during lactation and, therefore, should spend greater foraging effort to meet those demands. Female AFS displayed higher indices of diving effort, reduced patch residence times, and briefer postbout intervals, suggesting more effort spent foraging, and a faster rate of encounter with prey patches. An important premise of our analyses is that both species forage optimally, i.e. that they maximize energy intake rate relative to physiological constraints. Previous results have shown subtle interspecific differences in diet and dive depth associated with differences in life history and pup physiology (Luque et al. 2007a), so behavioural and physiological constraints may not be similar between AFS and SFS. Moreover, optimal foraging behaviour (e.g. time spent in foraging patches and patch encounter rate) may also differ between species, and affect their rates of energy intake. Our results largely support these predictions, and suggest a possible origin for the differences in foraging behaviour. We review the assumptions that were required to use our approach, and discuss the implications of our results for inferring the characteristics of the foraging habitat of sympatric AFS and SFS.

Assumptions

Using the information on differences in physiological constraints required making assumptions regarding the diving behaviour of fur seals (Mori et al. 2002, 2005, Mori & Boyd 2004b). A major assumption of the model is that energy intake is a function of time spent at the bottom of dives, i.e. prey is assumed to be obtained during the bottom phase of dives. Although it was not possible to ascertain the validity of this assumption with a 2-dimensional dive profile and sampling interval of 5 s, direction reversals (wiggles) during descent or ascent phases were rare. Furthermore, the mean vertical distance covered during the bottom phase of dives (a measure of the amount of wiggling) was relatively high for both species (AFS = 12.7 m; SFS = 15.0 m) for dive depths >10 m. These values exclude shallow V-shaped dives, which are indicative of travelling behaviour. Therefore, fur seals from La Mare aux Elephants probably concentrated their energy intake during bottom time.

A more fundamental assumption of the model is that fur seals dived optimally, so as to maximize the rate of energy intake during the dive cycle. Foragers may not always use an energy intake rate maximizing currency to behave optimally (Caraco 1980), as other factors may play important roles in determining what behaviour is optimal under particular time scales. Nonacs (2001) reviewed several studies testing predictions based on this assumption and found a consistent bias in the predictions, arguing that inclusion of the forager's state (e.g. nutritional status and predation risk) in the models can improve their predictive power. Heithaus & Frid (2003) proposed a model to account for predation risk during the surface interval for diving predators, which may partly explain why diving behaviour is often considered suboptimal in previously used models. Killer whales are common around Iles Crozet during summer (Guinet 1992), but they feed mainly on penguins and elephant seals at this location. Although the risk of predation on fur seals can be high in some populations (Boveng et al. 1998), it is probably low at Ile de la Possession, because no females identified at La Mare aux Elephants were lost while nursing a pup, nor were there visible wounds or scars that could have been inflicted by a predator. Nonetheless, studies to determine whether predation risk differentially affects foraging behaviour of sympatric fur seals at Ile de la Possession may provide further insights into the mechanisms driving the observed differences in foraging behaviour.

Closely related to predation risk, the nutritional status of fur seals could also potentially influence foraging behaviour because animals may trade off energy gain with safety from predators (Nonacs 2001, Wirsing et al. 2008). Direct measurements of fat, the primary form of energy storage in pinnipeds, are not available for our study animals. However, a concurrent study showed that foraging trips at Ile de La Possession were among the briefest reported for each species at comparable stages of lactation (Luque et al. 2007a). Furthermore, the large proportion of overnight foraging trips, the relative proximity (50 to 100 km) of foraging grounds (Bailleul et al. 2005), and the relatively fast growth rates of pups compared to other populations of both species, suggest that neither of them were under nutritional stress. Differences in energy stores between species under such conditions are expected to have minor influence on foraging behaviour (Houston et al. 1993, Nonacs 2001).

Behavioural versus physiological differences

We found conflicting evidence on the level of activity of fur seals, measured as the mean speed and absolute number of meters that fur seals swam during the bottom phase of dives. The former showed no differences between fur seal species, but the latter showed higher activity levels in SFS females. Speed is typically measured by counting the number of revolutions per unit time taken by a turbine on TDRs. These turbines are susceptible to clogging by debris (Shepard et al. 2008), rendering speed measurements for any given dive phase not as regular as depth measurements, despite similar sampling frequency. Consequently, fewer speed measurements were available for our comparisons of mean speed during any given dive phase, reducing the power of statistical comparisons relative to tests based on depth measurements. The vertical meters that fur seals swam per unit time during the bottom phase of dives may, thus, be a better index of activity level, and our results suggest that SFS females were more active during this phase. Despite the behavioural difference during the bottom phase of dives, SFS females showed increasing surface intervals following longer dives than AFS females.

Our data suggest that an important physiological parameter, the ADL, is higher in SFS than in AFS females. This result was unexpected and counter-intuitive because maximum dive depth was highest for AFS females, which was expected to be associated with a higher ADL. Lactating AFS females required exponentially longer periods at the surface when dive duration exceeded 150 s, while SFS females responded similarly, but to dives exceeding 250 s in duration. Consistent with these observations, SFS dived deeper and for longer periods of time, on average. ADL calculations based on direct measurements of oxygen stores and diving metabolic rates of fur seals from South Georgia (Costa et al. 2004) yielded a value (96 s) that is much lower than that reported here, especially considering the larger body mass of individuals in that study. However, our data cannot readily be compared with direct measurements of ADL, and factors such as exceeding the ADL during deep diving bouts could account for the difference. Unfortunately, similar data are not available for SFS females, but if the tendency of study individuals to exceed the ADL is similar, then the observed interspecific differences may parallel actual differences in ADL. Costa et al. (2004) suggest that the tendency of epipelagic feeders, such as AFS and SFS, to exceed the ADL are indeed expected to be similar and relatively low. Although direct measurements of diving metabolism are needed to corroborate our results, the differences illustrated in Fig. 4 are likely a result of actual differences in ADL.

Inferring foraging patch characteristics

Previous analyses suggest that AFS and SFS females from La Mare aux Elephants used similar foraging areas during the 2001 and 2002 breeding seasons (Bailleul et al. 2005). Dietary analyses (Luque et al. 2007a) indicate that these fur seals also feed on the same myctophid fish species, albeit in different proportions (Luque et al. 2007a). Similar results have been found in sympatric populations at Macquarie Island (Robinson et al. 2002). The present study suggests that differences in physiological constraints may have led to different temporal and vertical distribution of diving, despite similarities in horizontal distribution of foraging locations and prey species. Whereas AFS foraged between the surface and 20 m more frequently than SFS females, the latter foraged more extensively between 30 and 60 m. Furthermore, both species reduced the frequency of foraging below 80 m, although SFS females did so more rapidly, and dive bouts below 140 m were only observed in AFS females. Assuming that dive bouts reflect foraging in different prey patches, AFS females exploited more patches per night of foraging, and a larger fraction of patches close to the surface. It may have been more profitable for AFS females to rapidly move between different patches at shallow depths, thereby reducing mean dive time and, possibly, also the extent of anaerobic diving (Costa et al. 2004).

Similar segregation of foraging depth has been observed in macaroni *Eudyptes chrysolophus* and gentoo *Pygoscelis papua* penguins at Bird Island, South Georgia (Mori & Boyd 2004b), showing some analogies in their response with that of the fur seals in this study. Macaroni penguins increased surface times in response to briefer dive durations (Fig. 1 in Mori & Boyd 2004b), so their ADL is presumably lower than that of gentoo penguins. Macaroni penguins concentrated their foraging bouts at shallower depths compared to gentoo penguins, analogous to the higher frequencies of shallow bout depths observed in AFS compared to SFS females at La Mare aux Elephants. Although direct measurements of prey density and abundance at different depths were not available in the present study to validate an index of patch quality (IPQ; Mori & Boyd 2004a), this index can be calculated with the available data to examine potential interspecific differences in foraging patch quality. According to Mori & Boyd (2004a), energy intake rate (G) can be expressed in terms of dive duration (u) and travel time from/to the surface (τ) as $G = a \times (u - \tau)^x / (u + y(u))$, where $y(u)$ is surface time as a function of dive duration, obtained from Fig. 4, and a is an energy conversion constant. If divers regulate dive duration so as to maximize the rate of energy intake, the IPQ for a dive can be determined by finding the value of x that maximizes G. The IPQ thus calculated indicates that foraging patch quality is higher for AFS below 50 m, suggesting that this species foraged more profitably deeper in the water column than SFS (Fig. 5). Concurrent measurements of the distribution and densities of different prey species and the foraging behaviour of their air-breathing predators are needed to evaluate this suggestion.

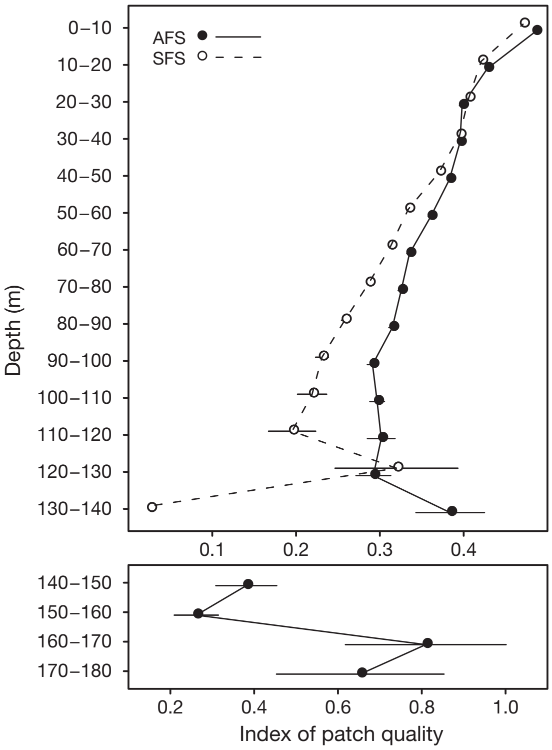

Fig. 5. *Arctocephalus gazella* (AFS), *A. tropicalis* (SFS). Lactating Antarctic fur seal (AFS) females encounter foraging patches with higher index of patch quality (IPQ) than subantarctic fur seal (SFS) females at depths between 50 and 100 m. They also exploit patches at depths >140 m, which are not used by SFS and where variation in IPQ is large. Data for each species were shifted in opposite directions by a small amount on the vertical axis (within the same depth class) to avoid overlap of points. Values are means ± SE

Since the IPQ may be similar between species at shallow depths, why did SFS females not exploit patches at these depths as extensively as AFS females did, despite their higher ADL? Conversely, why did AFS females exploit deep patches more extensively than their congenerics, despite their lower ADL?

Optimal diving models (Mori 1998a,b) predict that divers with higher ADLs should have deeper optimal foraging depth, for any given prey patch quality. These models also predict that anaerobic diving is favourable when the prey patch is deep and of high quality (Mori 1998b). SFS females may thus require higher prey patch qualities near the surface to dive optimally. Factors such as swimming mechanics (Fish et al. 2003, Sato et al. 2007), and searching and/or travelling behaviour (Hindell et al. 2002) may explain why these favourable conditions were encountered less frequently above 20 and below 80 m by SFS compared to AFS females. For instance, both young and adult AFS and SFS show significant differences in fore- and hind-flipper size and shape (Bester & Wilkinson 1989, Luque et al. 2007b). Supporting this conjecture, AFS females showed a larger proportion of isolated dives, suggesting that they searched for foraging patches more extensively. Interestingly, activity during the bottom foraging phase of dives was higher in SFS, although their behavioural ADL was higher. This suggests that differences in the relationship between surface interval and dive duration were a result of physiological, rather than behavioural, constraints. Otherwise, the behavioural ADL would have been lower in SFS. Further studies comparing foraging efficiency between these species should help explain this pattern.

Indeed, the briefer bout durations and postbout intervals, and the larger proportion of exploratory dives observed in AFS females, may allow them to sample prey patches near the surface more frequently, and provide better knowledge of foraging conditions in this part of the habitat (Charnov 1976). Dive traces from AFS females at La Mare aux Elephants display stronger diel changes in dive depth than those from SFS females (Appendix 1), so that AFS find their deepest foraging patches during the crepuscular vertical migration of their myctophid prey (Boyd et al. 1994, McCafferty et al. 1998, Luque et al. 2007a). Some myctophid fish species of this sector of the Southern Ocean are known to form denser patches at their deep daytime depth locations than during the night (Bost et al. 2002), when they are patchily distributed near the surface. AFS, and to a much lesser extent SFS, may profit from the more densely aggregated fish during dawn and dusk, as they shift between these depth locations and spatial organizations. Our observations, therefore, suggest that AFS females spent a larger fraction of foraging time in patches of higher quality, particularly after dusk and before dawn, both during OFTs and LFTs, even when costs may have been higher due to deep (Luque et al. 2007a), anaerobic diving.

To conclude, we have shown interspecific differences in the temporal distribution of diving and foraging depth between sympatric AFS and SFS, which are consistent with the hypothesis that lactation pressure is higher in AFS. The larger number of bouts, briefer postbout interval, and higher propensity to dive anaerobically in AFS, suggest more effort spent at foraging. Furthermore, AFS appeared to concentrate that effort in prey patches of higher quality. These differences were associated with lower ADL, briefer lactation, and higher pup energy demands in AFS. Gentry et al. (1986) hypothesized that a suite of fur seal life history traits, including foraging behaviour and lactation duration, follow a latitudinal gradient, ultimately being determined by environmental seasonality and predictability. Additional information from species inhabiting temperate latitudes indicate that prey ecology may be more important than latitude in influencing foraging and maternal behaviours (Francis et al. 1998). Moreover, our results suggest that intrinsic differences in physiological constraints and lactational demands play important roles in determining the fine-scale foraging behaviour in sympatric populations of some species, despite similarities in diet and prey ecology.

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Temporal structure of diving behaviour in sympatric Antarctic and subantarctic fur seals

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Appendix 1. Typical Antarctic and subantarctic fur seal dive profiles

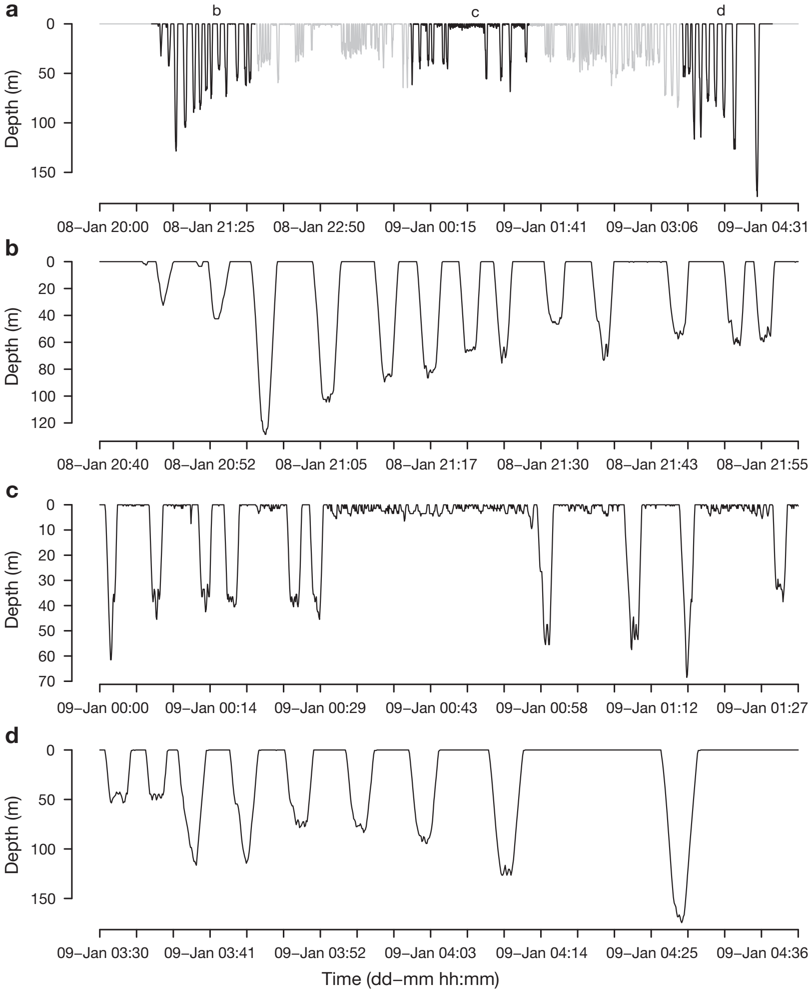

Fig. A1. *Arctocephalus gazella* (Antarctic fur seal). Typical dive profile of a lactating female showing strong nocturnal changes in depth: (a) an entire night of foraging (black lines denote zoomed region in subsequent panels), (b) dusk foraging, (c) midnight foraging, and (d) dawn foraging

Appendix 1 (continued)

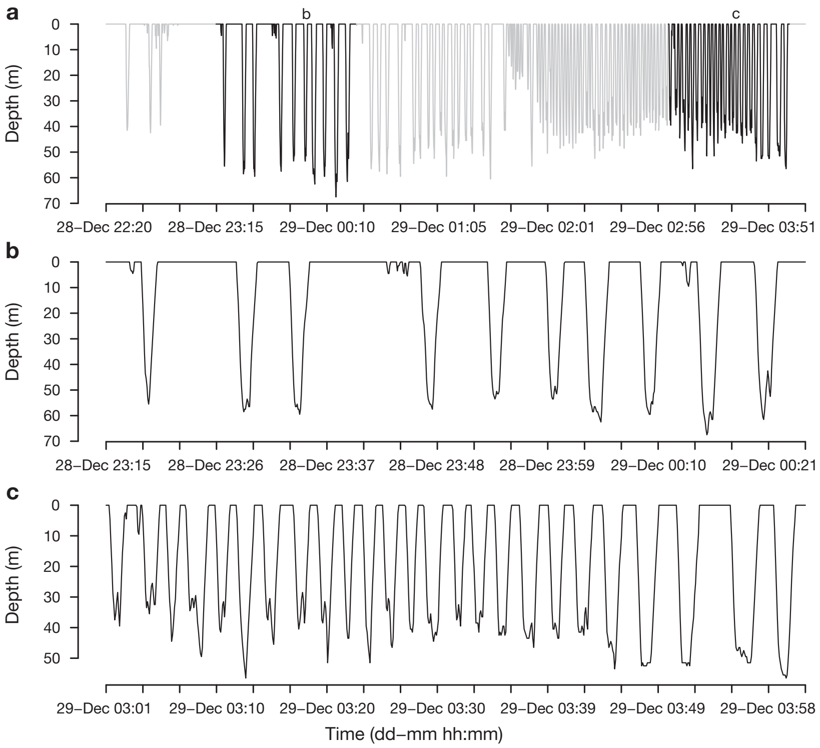

Fig. A2. *Arctocephalus tropicalis* (subantarctic fur seal). Typical dive profile of a lactating female showing little nocturnal changes in depth: (a) an entire night of foraging (black lines denote zoomed region in subsequent panels), (b) foraging before midnight, and (c) foraging after midnight

Part II

Allocation of maternal resources and pup development

Chapter 4

Ontogeny of body size and shape of Antarctic and subantarctic fur seals

Abstract

Pre- and postweaning functional demands on body size and shape of mammals are often in conflict, especially in species where weaning involves a change of habitat. Brief lactations are expected to be associated with fast rates of development and attainment of adult traits, compared to long lactations. We describe allometry and growth for several morphological traits in two closely related fur seal species with large differences in lactation duration at a sympatric site. Longitudinal data were collected from Antarctic (*Arctocephalus gazella* (Peters, 1875); 120-d lactation) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872); 300-d lactation) fur seals. Body mass was similar in neonates of both species, but *A. gazella* neonates were longer, less voluminous, and had larger foreflippers. The species were similar in rate of preweaning growth in body mass, but growth rates of linear variables were faster for *A. gazella* pups. Consequently, neonatal differences in body shape increased over lactation, and *A. gazella* pups approached adult body shape faster than did *A. tropicalis* pups. Our results indicate that preweaning growth is associated with significant changes in body shape, involving the acquisition of a longer, more slender

body with larger foreflippers in *A. gazella*. These differences suggest that *A. gazella* pups are physically more mature at approximately 100 d of age (close to weaning age) than *A. tropicalis* pups of the same age.

4.1 Introduction

Magnitude, rate, and pattern of mammalian growth determine adult body size and shape (Brody 1964, McNab 2002). Adult body size and shape, in turn, have major influences on viability and reproduction, among other life-history traits (Stearns 1992, Arendt 1997, Lindström 1999). Growth must be optimized relative to other demands, therefore it varies across individuals, populations, and species (Mangel and Stamps 2001, Caley and Schwarzkopf 2004). Some tradeoffs occur in offspring, and others are imposed by different tradeoffs acting on their mothers, which may alter the quality and quantity of milk they deliver. Interspecifically, milk composition and energy content are related to duration of lactation, so differences in the latter do not necessarily reflect total energy transferred to the offspring. Tilden and Oftedal (1997) noted that, in primates, the energy density of milk is inversely related to duration of lactation. Similarly, slowly growing and highly mobile offspring typify ungulate and macropod (kangaroos, wallabies, etc.) species with long lactations (Sæther and Gordon 1994, Fisher et al. 2002). However, body size is an important complicating factor, as lactation typically lasts longer in larger species (Peters et al. 1983, Clutton-Brock 1991*b*, Ross 1998). Because of these confounding factors, reasons for interspecific variation in growth with respect to lactation duration remain poorly understood.

Pinnipeds are an attractive model for studying preweaning development because they undergo a transition from suckling on land to foraging at sea, involving major physical, physiological, and behavioural changes in preparation for that transition.

The success of the transition ultimately depends on the acquisition of sufficient oxygen stores in relation to energy expenditure while diving (Burns and Castellini 1996, Burns 1999, Thorson et al. 1994, Horning and Trillmich 1997*a*,*b*). However, increased physiological diving capacity must be closely coordinated with physical growth and the gradual development of swimming skills (Jørgensen et al. 2001, Bowen et al. 1999). Recent studies suggest that, across a broad range of marine mammal species, oxygen storage capacity does not reach adult levels before independent foraging (Noren et al. 2001, Burns et al. 2004). Therefore, lactation duration is an important factor affecting the ontogeny of physical and behavioural traits of offspring.

Relationships between life-history traits have been extensively studied in pinnipeds because they are ecologically and reproductively diverse, and display a wide range of body sizes (Stirling and Kleiman 1983, Bonner 1984, Oftedal et al. 1987, Costa 1993, McLaren 1993, Boyd 1998). For instance, lactation lasts from < 4 d (hooded seal, *Cystophora cristata* (Erxleben, 1777)) to 2-3 yr (walrus, *Odobenus rosmarus* (L., 1758)). Quality of knowledge, however, varies across species; good estimates of lactation duration are available for only eight species; three otariids and five phocids (Schulz 2004). Good quantitative estimates of growth rate and duration of lactation for the same species are available for even fewer. Considering the difficulty in obtaining comprehensive and precise data, and given the widespread effects of spatiotemporal environmental variability on one-time estimates (Trillmich et al. 1991*a*, Lunn et al. 1993), an alternative approach for comparing ecologically different and related species might be profitable. Two otariid species that have recently been used in the context of foraging and growth studies are the Antarctic (*Arctocephalus gazella* (Peters, 1875); AFS hereafter) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872); SFS hereafter) fur seals (Kerley 1985, Goldsworthy et al. 1997, Klages and Bester 1998, Goldsworthy and Crowley 1999, Robinson et al. 2002).

We investigated comparative growth in AFS and SFS pups to determine the presence and nature of differences that may influence how the species cope with the critical postweaning period, as pups become independent foragers. These species have similar adult body mass and length (Payne 1979, Bester and Van Jaarsveld 1994), yet exhibit a large disparity in lactation duration: 116 in AFS (Costa et al. 1988, Lunn et al. 1993) and 300 d in SFS (Kerley 1987, Guinet and Georges 2000), respectively. Therefore, the time required to acquire the physical and physiological characteristics enabling pups to become independent foragers may differ between the species. Comparisons between two species species cannot be used to elucidate the relationship between lactation duration and growth patterns, but offer an advantage that is rarely found in multispecies comparisons: the ability to control for confounding factors, such as environmental differences between populations of different species, in syntopic (locally sympatric) populations. AFS and SFS breed syntopically at a few locations, where habitat differences between species are likely to be minimal, facilitating the interpretation of comparative analyses.

In previous research, Arnould et al. (2003) found that daily pup energy expenditure was higher in AFS than in SFS breeding syntopically at Ile de la Possession, Crozet archipelago, in the Southern Indian Ocean. In contrast, earlier reports from other syntopic sites suggested higher growth rates in body mass of AFS (Kerley 1985, Goldsworthy and Crowley 1999). We suggest that the reported disparity may reflect differences in body shape, which commonly differs adaptively between related species (Dodson 1975, Carrier 1983, Alatalo et al. 1984, Atchley 1984, Creighton and Strauss 1986, Gisbert 1999, Hochuli 2001).

Functional demands on body size and shape may change sharply between pre- and postweaning ages in young pinnipeds, especially in otariids because of their long preweaning terrestrial existence (Koehler and Barclay 2000). Within the otariids, AFS and SFS differ substantially in this regard, so we predicted that these species would differ in growth trajectories and in the rate at which they acquire adult body form or shape (e.g., in foreflippers; Fish 1998, Fish et al. 2003). Specifically, we predicted that AFS pups should acquire adult flipper size and shape relatively sooner than SFS, assuming that this allows them to make a successful transition to independent foraging at an earlier age.

4.2 Materials and methods

4.2.1 Fur seal colonies and identification procedures

Research was carried out at La Mare aux Elephants (46°22’29” S, 51°40’13” E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001-02 (4 December - 25 March) and 2002-03 (1 December - 16 March) breeding seasons (2001 and 2002 hereafter). The site consists of two adjacent AFS and SFS colonies on different types of substrate: AFS on the northern part of the beach, composed of small- to medium-sized pebbles, with gentle slopes behind; and SFS on the southern part of the beach, composed of large boulders that have fallen from the steep hinterlands. Both species give birth close to shore, but the AFS colony grows in size as the season progresses, while the other species tends to remain close to shore during the same period.

Pups were individually marked (Georges and Guinet 2000*a*, Arnould et al. 2003, Bailleul et al. 2005) over a 6- (2001) or 13- (2002) day period (Table 4.1). Pup production and mean pupping date were estimated using total pup counts (both years; including dead and living pups) on a weekly basis until no more births were observed, and mark-recapture methods (2001 only). Peak pupping dates were 5 and 15 December (2001: 164, and 2002: 167 pups) for AFS, and 25 and 30 December

(2001: 80, and 2002: 91 pups) for SFS. Populations of both species have been increasing at an annual rate of about 18% annually at least until 1994 (Guinet et al. 1994).

4.2.2 Morphometric measurements

Body mass (BM) of pups was measured to the nearest 0.05 kg at first capture, and every 5-9 d thereafter, on a 25-kg capacity digital suspension balance (Salter Brecknell, ElectroSamson). The following variables were also measured on pups upon first capture and every 12-16 d thereafter: body length (BL; nearest 0.5 cm, straight line from the tip of the nose to the flesh tip of the tail) with a tape measure, while animals were manually restrained over a board, and positioned straight and flat on their ventral surface. In 2002, we also measured the following variables (nearest 0.5 cm) taken the same way, and on the same schedule: body girth at levels of pinna, mid neck, axillae, and umbilicus (G1-G4, hereafter); distance from the tip of the nose to each of these points (see next; RL1-RL4, hereafter). BL and RL1-RL4 were measured with a straight tape measure glued onto the board on which animals were placed. Length, width, and surface area of foreflippers were measured as follows. First, the right foreflipper was extended and held to the side of and perpendicular to the body, and was placed on a wooden board with horizontal and vertical scales (20 cm, marked every 5 cm). Second, a photograph was taken (Nikon Coolpix E885) in dorsal aspect from a distance of approximately 1.25 m. Finally, measurements were made from the photographs: (1) length (FL), defined as the distance from proximal end of the humerus (estimated by palpation) to the tip of foreflipper, through the midline of the flipper; (2) width (FW), defined as the largest distance, perpendicular to foreflipper length; and (3) area (FA; estimated from the traced outline of the foreflipper, using Object-Image, version 2.11, U.S. National Institutes of Health, available from `http://simon.bio.uva.nl/object-image.html`). FL and FW were also measured directly on the foreflipper for cross-validation and subsequent analyses.

The relationship between direct measurements on flippers, and those taken photogrammetrically, were tested for linearity to detect outliers or invalid estimates. This led to the exclusion of FA estimates for pups with FL $>$ 27 cm, as the corresponding relationship became asymptotic beyond this value, indicating decreasing accuracy.

We also took all measurements on 63 AFS and 70 SFS adult females, but BM was measured to the nearest 0.5 kg. Each female was measured at least twice, and the median value for each variable was used to set adult body measurements, for comparisons with pups. Estimates for some variables on adult males were included using data taken at South Georgia for AFS (Payne 1979) and at Marion Island (about 950 km west of Crozet) for SFS (Bester and Van Jaarsveld 1994).

Body volume (BV; ± 0.01 l) of pups was obtained by using model B in Luque and Aurioles-Gamboa (2001), in which the body was modelled as two cones plus two truncated cones. Volumes of cones ($\frac{1}{3}\pi h[r_1^2+r_2^2+r_1^2 r_2^2]$) and truncated cones ($\frac{1}{3}[\pi r^2 h]$) were calculated using the lengths (h) of cones estimated from RL1 and RL4, and lengths of truncated cones were estimated from RL2 and RL3, respectively. Girth was used to calculate radius (r).

4.2.3 Analyses

Interspecific differences in neonatal and adult body size were assessed using double classification analyses of variance, with a term for sex effects, including only data for which accurate ages were available. However, adult females were assigned to a single age category because their ages were unknown.

To determine whether growth trajectories varied according to species or sex, a linear mixed effects model (Raudenbush and Bryk 2002) was designed for the jth observation on the ith individual:

$$\begin{aligned} y_{ij} = & [\beta_{00} + \beta_{01}\text{species}_i + \beta_{02}\text{sex}_i + \beta_{03}\text{species}_i\text{sex}_i + b_{i0}] + \\ & [\beta_{10} + \beta_{11}\text{species}_i + \beta_{12}\text{sex}_i + \beta_{13}\text{species}_i\text{sex}_i + b_{i1}]x_{ij} + \varepsilon_{ij} \end{aligned} \tag{4.1}$$

where β_{00} and β_{10} refer to the population intercept and slope, respectively, for AFS female pups, the baseline group. β_{01}, β_{02}, and β_{03} are fixed effects for the change in population intercept associated with the species, sex, and their interaction, in relation to the baseline group. β_{11}, β_{12}, and β_{13} are the changes in population slope associated with the same effects. b_{i0} and b_{i1} are the random intercept and slope effects for the ith individual, respectively, and ε_{ij} is a within-subject residual term. Other terms were added to test for year effects and their interactions with body mass and body length, but were subsequently dropped if they were non-significant here and elsewhere, at $\alpha = 0.05$.

Based on exploratory analyses and because ages were < 300 d, a linear model was assumed, rather than a more complicated one. No assumptions were made regarding the autocorrelation structure of the ε_{ij}'s. However, it was assumed that these were independent and normally distributed, regardless of the b_i's. In this model, species_i and sex_i take on values zero and one, to indicate whether y_{ij} refers to AFS or SFS, and to a female or a male pup, respectively. We fitted the model using a restricted log-likelihood method, as described in Pinheiro and Bates (2000), and implemented in the nlme R package (Pinheiro et al. 2004). We subsequently estimated linear equations from this model, collapsing across and (or) within fixed effects that were not significantly different from zero. Only pups that were measured more than twice throughout the study period were considered for these analyses.

Because absolute age was not known for all individuals (Table 4.1), relative age was defined as the number of days elapsed since seals were first seen, which was taken as day zero. The difference in peak pupping dates between species was taken into account by adding the corresponding value from each breeding season (2001: 20, and 2002: 15 d) to the relative age of Antarctic fur seal (AFS) pups. Relative age was then used as the regressor x in model (4.1). Relative age was logarithmically transformed (logarithm base 10), and a constant added to it, to achieve linearity before using it as the regressor for BL in model (4.1). This transformation was chosen because BL changed faster in young pups (< 30 d) than older pups.

To address the question of whether growth trajectories gave rise to interspecific differences in the rate at which pups acquired adult body shape, two allometric relationships that might influence aquatic locomotory performance (e.g. Feldkamp 1987, Fish et al. 1988, Stelle et al. 2000) were studied: (1) foreflipper span (FS; see next) squared vs total FA (TFA; see next), and (2) RL3 vs BL. FS was calculated as $2 \cdot \mathrm{FL}+\mathrm{G3} \cdot \pi^{-1}$, and TFA as $2 \cdot \mathrm{FA}$. The first relationship is foreflipper aspect ratio expressed allometrically, whereas the second was used as an index of the position of foreflippers along the body axis, relative to BL. One random measurement per female pup where $80 \text{ d} < \text{age} < 120$ d, was selected for this analysis, to eliminate any dependence between observations, while maintaining a large enough sample size with valid foreflipper measurements (i.e. < 27 cm). For adult females, the median value for each variable was used, assuming their growth was negligible.

To investigate how allometric relationships (1) and (2) compared between species and age groups (female pups vs adult females), we used analysis of covariance (Zar 1996). We were interested in the interaction between age group (adult or pup) and species to test whether pups of one species were more allometrically similar to adults than the other. This approach avoided known biases associated with ratios between the variables from each relationship (Packard and Boardman 1999).

All statistical analyses were performed in the GNU R system (R development Core Team 2007). Shapiro-Wilks statistic and Fligner-Killeen test were used to evaluate assumptions of normality of data distributions and homogeneity of variances, respectively, in analyses of variance and covariance. Results show SE as the measure of dispersion, unless stated otherwise.

4.3 Results

4.3.1 Neonatal and adult body size

There was no evidence of interannual effects on neonatal BM ($F_{1,160} = 1.70, P = 0.19$) nor body length ($F_{1,157} = 2.03, P = 0.16$), when species and sex were taken into account. Therefore, measurements were pooled across years for subsequent analyses.

Male neonates were larger than females in most measurements (Table 4.2). AFS neonates were significantly longer than SFS neonates, had longer head and neck regions (RL1 and RL2), longer and narrower foreflippers, and greater FA (Table 4.2). Other interspecific differences were found among females only; AFS female pups were larger in girth and BV than SFS pups. Adult female AFS were significantly heavier than SFS. AFS adult females were larger in all flipper measurements than SFS adult females (Table 4.3).

4.3.2 Growth

Growth trajectories for each variable showed differing patterns of growth between species. No main effects or interactions of year with species or sex effects were significant in the models of mass and body length growth ($P > 0.5$, all cases), so the data were pooled. The magnitude and standard error of interspecific and intersexual effects, in terms of model (4.1), are shown in Table 4.4. Estimated growth rates for each variable, with results of interspecific comparisons, are shown in Table 4.5.

In both species, sexual differences in BM increased steadily throughout lactation due to faster growth of male pups ($t_{2822} = 4.0$, $P < 0.01$). However, pups grew at a similar rate in both species ($t_{2822} = -0.04$, $P > 0.90$), after sex effects were removed (Figure 4.1). Neonatal BM did not differ between species, but the intercept of the relationship between BM and relative age was higher in AFS pups. No interactions were significant between species and sex ($t_{264} = -1.34$, $P > 0.1$; $t_{2822} = 0.18$, $P > 0.8$, respectively). A similar pattern was found for BV (Figure 4.1), consistent with faster rates of growth in SFS girth (Table 4.5).

Growth in BL was faster in AFS pups ($t_{1321} = -2.57$, $P = 0.01$), and in males of both species ($t_{1321} = 2.21$, $P = 0.03$) (Figure 4.1). There were no interactions between species and sex for slope ($t_{1321} = -0.05$, $P > 0.9$) or intercept ($t_{260} = -0.93$, $P > 0.3$). RL1 and RL2 showed faster rates of growth in AFS ($t_{441} = -4.65; -2.80$, $P < 0.01$, both cases), irrespective of sex ($t_{441} = 1.49; 1.53$, $P > 0.1$) (Table 4.5).

All foreflipper measurements increased in size faster in AFS: FL and FW ($t_{441} = -10.50; -2.45$, $P < 0.02$, both variables); FA ($t_{208} = -5.13$, $P < 0.01$) (Figure 4.2). There were no significant interactions with sex (FL and FW: $t_{441} = 0.96; 1.92$, $P > 0.3$, FA: $t_{208} = 0.47$, $P > 0.6$).

4.3.3 Allometry

Pup growth trajectories along individual variables led to differing allometric relationships between species and age groups. A two-way analysis of covariance indicated that age-group differences in the slope of the relationship between FS^2 and TFA were dependent of species ($F_{1,43} = 5.00$, $P = 0.03$, slope interaction term). Age-group did not significantly affect the allometric slope ($F_{1,27} = 2.83$, $P = 0.10$) in AFS, but it did in SFS ($F_{1,16} = 5.29$, $P = 0.04$); female SFS pups had a higher allometric slope than adult females (Figure 4.3a). Among pups, the allometric slope showed large differences between species ($F_{1,25} = 11.4$, $P = 0.002$), but it was similar between species among adults ($F_{1,18} = 0.36$, $P = 0.55$). In agreement with this trend, differences in the allometric slope between pups and adults were larger in SFS. Foreflipper size differences between pups and adults were also much larger in SFS.

RL3 scaled with BL differently between species ($F_{1,69} = 6.01$, $P = 0.02$), but similarly between age-groups ($F_{1,69} = 0.29$, $P = 0.59$), without any interaction between these factors ($F_{1,65} = 1.08$, $P = 0.30$). The allometric slope of the relationship was higher in AFS, particularly among female pups (Figure 4.3b).

4.4 Discussion

4.4.1 Neonatal and adult body size

Based on multiple traits, we documented many interspecific differences in neonatal body size, preweaning growth, and changes in body growth between two otariid species, AFS and SFS. We hypothesized that AFS pups should mature physically faster than SFS pups, given their younger weaning age. Neonates of the two species differed little on any measurements, but differed greatly in rates of growth. However, if adults show larger differences between species than neonates, the results may simply reflect intrinsic morphological differences between species, rather than different development patterns. Therefore, we begin our discussion by comparing neonate and adult body size of AFS and SFS at Iles Crozet with other populations, and then focus on the factors that could have given rise to species differences in development.

We found no species differences in neonatal body mass at Iles Crozet, as Kerley (1985) also found for seven animals at Marion Island. No comparable data are available from Macquarie Island, the third site where the two species coexist. However, body mass alone cannot be used to compare body size between the species, because neonatal body shape differs: at birth, AFS pups are longer, have longer heads and necks, and have larger foreflippers. Therefore, the similarity between species in body mass may indicate differences in body composition, rather than similarities in body size. Based on a small sample of our pups from 2001, Arnould et al. (2003) showed that AFS pups had lower total body lipid stores than SFS pups at approximately two months of age, and our results suggest that the difference may also be present at birth.

Neonates of both species from our study were about a kilogram heavier than those weighed by (Kerley 1985), although the difference cannot readily be attributed to any ecological factor due to the small sample size in the latter study. Estimated pup birth dates in our study were similar to those reported by Kerley (1985) on Marion Island, consistent with Sparrow et al. (1996), who showed that the two archipelagoes have a similar marine environment. The body mass of neonatal SFS pups in our study is comparable to that obtained from allopatric sites at Amsterdam Island (Georges and Guinet 2000*a*) and Gough Island (Bester 1987, Bester and Van Jaarsveld 1994) for SFS, and at Bird Island, South Georgia (Lunn et al. 1993) for AFS, suggesting that adult females are equally able to meet the demands of gestation in these environments, or can compensate for any differences without a cost to newborn offspring.

Sexual differences in neonatal body size occur in all otariids, including our species (Bester 1987, Kerley 1985, Lunn et al. 1993). However, pup sex did not influence most interspecific comparisons of neonatal body size in our analyses; sexual-size differences were similar for both species, except for girth measurements, body volume, and foreflipper surface area. For the latter three variables, AFS pups were larger than their congenerics only among females. The larger axillary girth and body volume of female AFS pups may reflect sex-specific differences in relative body lipid stores. Several authors have reported higher total body lipid stores in female, compared to male pups in several species (e.g. Arnould et al. 1996*a*, Donohue et al. 2002, Beauplet et al. 2003), including those in this study. Therefore, everything else being equal, female pups would be expected to be more voluminous than male pups (Luque and Aurioles Gamboa 2002).

Intraspecifically in pinnipeds, large mothers tend to give birth to large pups (Costa et al. 1988, Arnbom et al. 1997, Mellish et al. 1999). Boltnev and York (2001) found that neonatal mass increases at a decelerating rate with maternal mass in northern fur seals (*Callorhinus ursinus* (L., 1758)). The same relationship appears to hold interspecifically (Costa 1991), but whether the relationship is linear or not is unclear. Adult female AFS did not give birth to heavier pups in our study, despite being heavier than adult female SFS. Compared to body mass, linear measurements (body length, axillary girth, and RL3) of physically restrained fur seals include larger measurement errors, reducing the statistical power of interspecific comparisons. Therefore, comparisons of pup body size in relation to maternal body size require more accurate measurements.

Both adult females and neonates differed in body shape between species, so interspecific differences in growth of body size may simply reflect morphological differences between AFS and SFS. We did not measure adult males of both species at La Mare aux Elephants, so we cannot generalize the argument to both sexes. However, if growth rates of individual variables were mainly determined by species-specific morphometric traits, then interspecific differences in these traits would be expected to be similar in neonates and adults, and body shape would be expected to remain relatively constant with age. Both expectations from this argument were not supported by our results. The magnitude of morphometric differences between species were considerably larger among adult females than among neonates, and more similarities in body shape between adult females and 80-120 d old pups were found in AFS than in SFS. Therefore, the growth patterns exhibited by each species may not be only related to intrinsic morphometric differences between them.

4.4.2 Preweaning growth and allometry

We found no interspecific differences in rate of growth in body mass. This contrasts with previous studies of these species where they are sympatric (Marion Island: Kerley (1985); Macquarie Island: Goldsworthy and Crowley (1999)). Our estimates of growth rates in body mass also were lower at Ile de la Possession than at those two sites. The reasons for such discrepancy are not clear, but methodological differences in pup sampling protocol (longitudinal vs cross-sectional) and period of lactation covered hinder the comparison of results among these studies.

In our study, SFS and AFS pups had similar rates of growth in body mass and body volume. However, AFS pups had: (1) faster rates of growth in body length, length of anterior portions of the body (RL1-RL2), and foreflipper dimensions, and (2) lower rates of growth in body girth. These differences lead to a more streamlined body with relatively large foreflippers in AFS, and a stockier body in SFS.

Two-species comparisons cannot provide general conclusions about relations between lactation duration and growth pattern (Garland and Adolph 1994) in otariids, but by minimizing other confounding factors, such a comparison can provide insights into possible mechanisms (Fisher et al. 2002). We hypothesized that AFS pups would exhibit more precocial growth than SFS pups. In AFS, differences between pup and adult foreflipper shape, and their position along the body, differed more than in SFS, which supports this hypothesis. These differences were reflected in the relationship between foreflipper span^2 and foreflipper surface area, which defines an important measure (aspect ratio) of aquatic locomotory ability (e.g. Feldkamp 1987, Fish et al. 1988, Norberg et al. 1993). For instance, low-aspect ratio flippers are associated with increased costs of transport during steady swimming, but are better suited for rapid accelerations during quick turns in open water (Fish and Nicastro 2003, Fish et al. 2003). A similar argument can be made for the relationship between RL3 and body length, which is an index of the position of the foreflippers along the body. Relative position of the foreflippers along the body may have functional significance in aquatic stability and maneuverability, which is favoured when foreflippers are located far from the center of gravity (Fish et al. 2003).

Allometric analysis (Fig. 4.3) suggests that AFS pups have foreplippers positioned more posteriorly along the body, and lower foreflipper aspect ratio than SFS pups, and hence potentially greater aquatic turning abilities at 100 d (± 20) of age. However, while AFS pups are near the end of lactation at this age, SFS pups are in mid-lactation, so increased aquatic turning abilities may be more critical for the former. Indeed, the largest foreflipper surface areas of female AFS pups were close to adult values, which was not the case for female SFS pups. Further studies are needed to assess the effect of differences in flipper size and structure for terrestrial locomotion, and the acquisition of foraging skills at sea of these two species. Other factors that are likely to influence this process, such as the timing and pattern of moulting, should also be considered because they are known to affect pup thermoregulatory ability (Donohue et al. 2000).

To summarize, we found many differences in growth of AFS and SFS pups at Iles Crozet, where the species breed sympatrically, but maintain species-specific differences in lactation duration. Compared to SFS pups, AFS pups adopted a growth strategy that favours the acquisition of a longer, more slender body, with larger foreflippers. The growth differences between species led to different allometric relationships between female pups and adult females, whereby AFS pups showed more similarities in foreflipper shape and position along the body with their adult counterparts than SFS pups. These interspecific comparisons of allometric relationships suggest AFS pups are physically more mature at approximately 100 d of age (close to weaning age) than SFS pups of the same age. Whether SFS pups achieve a similar level of physical maturity close to their weaning age, and whether different morphological development patterns affect the ontogeny of foraging skills, remain to be determined.

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Table 4.1. Summary of numbers of Antarctic (*Arctocephalus gazella* (Peters, 1875); AFS) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872); SFS) fur seal used in the study, broken down by year, species, and sex. Cell entries indicate total number, including newborn pups; number of newborn pups is shown in parentheses

Species	Sex	Breeding season		
		2001	2002	Both
AFS	Females	47 (10)	29 (24)	76
	Males	48 (6)	29 (19)	77
	Both	95	58	153
SFS	Females	31 (27)	36 (32)	67
	Males	27 (22)	30 (28)	57
	Both	58	66	124

Table 4.2. Summary of morphometric differences between species and sexes in neonatal Antarctic (AFS) and subantarctic (SFS) fur seals. Sample sizes (n; females, males) were: AFS $n = 22$, 17; SFS: $n = 32$, 28 for all variables, except for body mass and body length, for which AFS $n = 34$, 25; SFS $n = 59$, 50

Variable		Females		Males		*F-ratio*[a]
		AFS	SFS	AFS	SFS	
Body mass (kg)	BM	4.90 ± 0.150	4.60 ± 0.080	5.40 ± 0.210	5.45 ± 0.100	0.98; **35.28**
Body length (cm)	BL	60.3 ± 0.54	58.8 ± 0.32	63.8 ± 0.75	61.7 ± 0.40	**11.34**; **46.63**
Girth (cm)	G1	30.4 ± 0.30^b	28.9 ± 0.14	30.6 ± 0.26	30.4 ± 0.15	**9.57**
	G2	29.5 ± 0.32^b	27.4 ± 0.26	28.6 ± 0.48	29.2 ± 0.27	**16.22**
	G3	39.6 ± 0.54^b	37.2 ± 0.33	39.3 ± 0.71	39.6 ± 0.43	**7.87**
	G4	39.1 ± 0.64^b	36.7 ± 0.41	39.1 ± 0.72	40.2 ± 0.55	**9.27**
Reference length (cm)	RL1	8.3 ± 0.13	7.8 ± 0.11	8.8 ± 0.17	8.1 ± 0.11	**25.33**; **9.24**
	RL2	12.9 ± 0.15	12.1 ± 0.16	13.6 ± 0.30	12.8 ± 0.19	**16.86**; **14.16**
	RL3	30.3 ± 0.41	29.0 ± 0.37	31.1 ± 0.62	30.9 ± 0.43	2.45; **11.15**
	RL4	43.8 ± 0.43	40.2 ± 0.34	45.0 ± 0.59	41.9 ± 0.37	**62.84**; **13.99**
Foreflipper length (cm)	FL	22.2 ± 0.23	21.1 ± 0.14	23.0 ± 0.45	22.0 ± 0.18	**21.66**; **13.77**
Foreflipper width (cm)	FW	8.0 ± 0.11	8.2 ± 0.10	8.4 ± 0.17	8.8 ± 0.10	**10.95**; **24.10**
Foreflipper surface area (cm^2)	FA	142.1 ± 3.57^b	126.6 ± 2.41	145.4 ± 5.99	144.1 ± 2.50	**4.30**
Body volume (l)	BV	4.5 ± 0.15^b	3.6 ± 0.08	4.5 ± 0.21	4.2 ± 0.11	**4.93**

[a] Values for interspecific and intersexual comparisons (respectively) are shown. Significant effects are in bold. For significant interactions, only the value for the interaction is shown

[b] For significant interactions, this is the species and sex with the highest mean

Table 4.3. Summary of morphometric differences between adult Antarctic (AFS) and subantarctic (SFS) fur seal females. Cell entries are Mean ± SE (*n*)

Variable		AFS	SFS	*F-ratio*[a]
Body mass (kg)	BM	32.7 ± 0.36 (63)	30.5 ± 0.45 (70)	**6.88**
Body length (cm)	BL	118.0 ± 0.49 (63)	117.0 ± 0.51 (70)	1.07
Axillary girth (cm)	G3	75.0 ± 0.70 (24)	73.8 ± 1.12 (22)	0.44
Reference length (cm)	RL3	63.3 ± 0.52 (24)	61.6 ± 0.55 (18)	2.74
Foreflipper length (cm)	FL	40.3 ± 0.25 (62)	33.9 ± 0.23 (70)	**179.80**
Foreflipper width (cm)	FW	12.9 ± 0.08 (62)	11.9 ± 0.07 (70)	**43.8**
Foreflipper surface area (cm^2)	FA	431.5 ± 11.46 (16)	348.1 ± 6.4 (11)	**17.67**

[a] Significant effects are in bold

Table 4.4. Summary of effects of species (β_{01} and β_{11}), sex (β_{02} and β_{12}), and their interactions (β_{03}) on growth of Antarctic and subantarctic fur seal pups, estimated using model (4.1) [a]. SE is in parentheses

Variable		Intercept effects			Slope effects	
		β_{01}	β_{02}	β_{03}	β_{11}	β_{12}
Body Mass (kg)	BM	**-0.950 (0.180)**		n.s.	n.s.	**0.010 (0.003)**
Body length[b]	BL			n.s.	**-1.740 (0.680)**	**1.410 (0.640)**
Foreflipper length	FL		**0.880 (0.330)**	n.s.	**-0.040 (0.004)**	n.s.
Foreflipper width	FW	n.s.	**0.570 (0.140)**	n.s.	**-0.004 (0.001)**	n.s.
Foreflipper surface area	FA		n.s.	n.s.	**-0.410 (0.080)**	n.s.
Body volume	BV	**-1.030 (0.230)**		n.s.	n.s.	**0.010 (0.004)**
Girth	G1	**-1.400 (0.300)**	**0.860 (0.310)**	n.s.	n.s.	n.s.
Girth	G2		n.s.	**1.700 (0.750)**	**0.040 (0.008)**	n.s.
Girth	G3		n.s.	n.s.	**0.030 (0.010)**	n.s.
Girth	G4		n.s.	n.s.	**0.060 (0.015)**	n.s.
Reference length	RL1		**0.550 (0.190)**	n.s.	**-0.010 (0.003)**	n.s.
	RL2		**1.150 (0.310)**	n.s.	**-0.020 (0.006)**	n.s.
	RL3	**-2.770 (0.580)**	**1.530 (0.590)**	n.s.	n.s.	n.s.
	RL4	**-4.070 (0.590)**		n.s.	n.s.	n.s.

[a] Interactions in slopes β_{13} were non-significant, so were omitted. Significant effects are in bold, n.s. = non-significant effect, and meaningless effects (due to interactions) were left blank

[b] Relative age (d) was log-transformed to linearize this relationship

Table 4.5. Comparison of growth rates of Antarctic (AFS) and subantarctic (SFS) fur seal pups, estimated using model (4.1). Cell entries are the estimated slope taken from the model (lower - upper 95% confidence limits)

Variable		Females		Males	
		AFS	SFS	AFS	SFS
Body mass (kg · d^{-1})	BM	0.06 (0.06 - 0.07)^{a}		0.08 (0.07 - 0.08)^{a}	
Body length (cm · log d^{-1})	BL	17.58 (16.68 - 18.47)	15.83 (14.85 - 16.82)	18.99 (18.11 - 19.86)	17.19 (16.15 - 18.23)
Girth (cm · d^{-1})	G1	0.04 (0.04 - 0.05)^{b}			
	G2	0.07 (0.06 - 0.08)	0.10 (0.09 - 0.11)	0.09 (0.07 - 0.10)	0.10 (0.09 - 0.1)
	G3	0.14 (0.13 - 0.15)	0.17 (0.15 - 0.18)	0.14 (0.13 - 0.15)	0.17 (0.15 - 0.18)
	G4	0.09 (0.08 - 0.11)	0.15 (0.13 - 0.18)	0.09 (0.08 - 0.11)	0.15 (0.13 - 0.18)
Reference length (cm · d^{-1})	RL1	0.05 (0.05 - 0.06)	0.04 (0.03 - 0.04)	0.05 (0.05 - 0.06)	0.04 (0.03 - 0.04)
	RL2	0.10 (0.10 - 0.11)	0.09 (0.08 - 0.10)	0.10 (0.10 - 0.11)	0.09 (0.08 - 0.10)
	RL3	0.10 (0.09 - 0.11)^{b}			
	RL4	0.13 (0.13 - 0.14)^{b}			
Foreflipper length (cm · d^{-1})	FL	0.08 (0.08 - 0.08)	0.04 (0.03 - 0.05)	0.08 (0.08 - 0.08)	0.04 (0.03 - 0.05)
Foreflipper width (cm · d^{-1})	FW	0.02 (0.02 - 0.02)	0.02 (0.02 - 0.02)	0.02 (0.02 - 0.02)	0.02 (0.02 - 0.02)
Foreflipper surface area (cm^{2} · d^{-1})	FA	0.99 (0.89 - 1.09)	0.58 (0.45 - 0.72)	0.99 (0.89 - 1.09)	0.58 (0.45 - 0.72)
Body volume (l · d^{-1})	BV	0.04 (0.03 - 0.04)^{a}		0.04 (0.04 - 0.05)^{a}	

[a] Growth rate was common to both species

[b] Growth rate was common to both species and both sexes

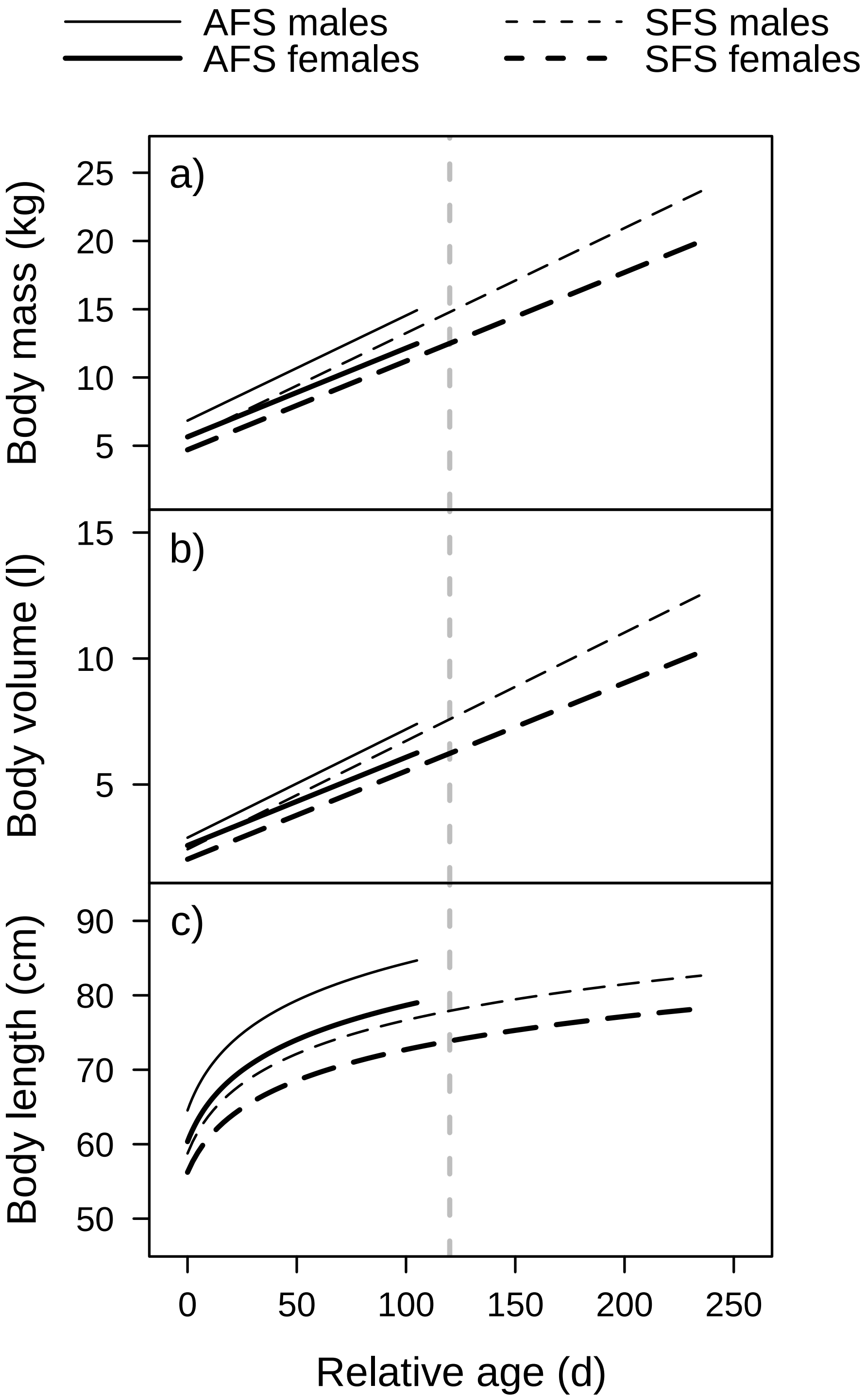

Figure 4.1. Rates of growth in a) body mass and b) body volume did not differ between Antarctic (AFS) and subantarctic (SFS) fur seal pups during lactation, but growth in c) body length was faster in AFS pups, based on equation (4.1). The vertical dotted line indicates the weaning age of AFS pups. See Table 4.5 for estimated growth rates

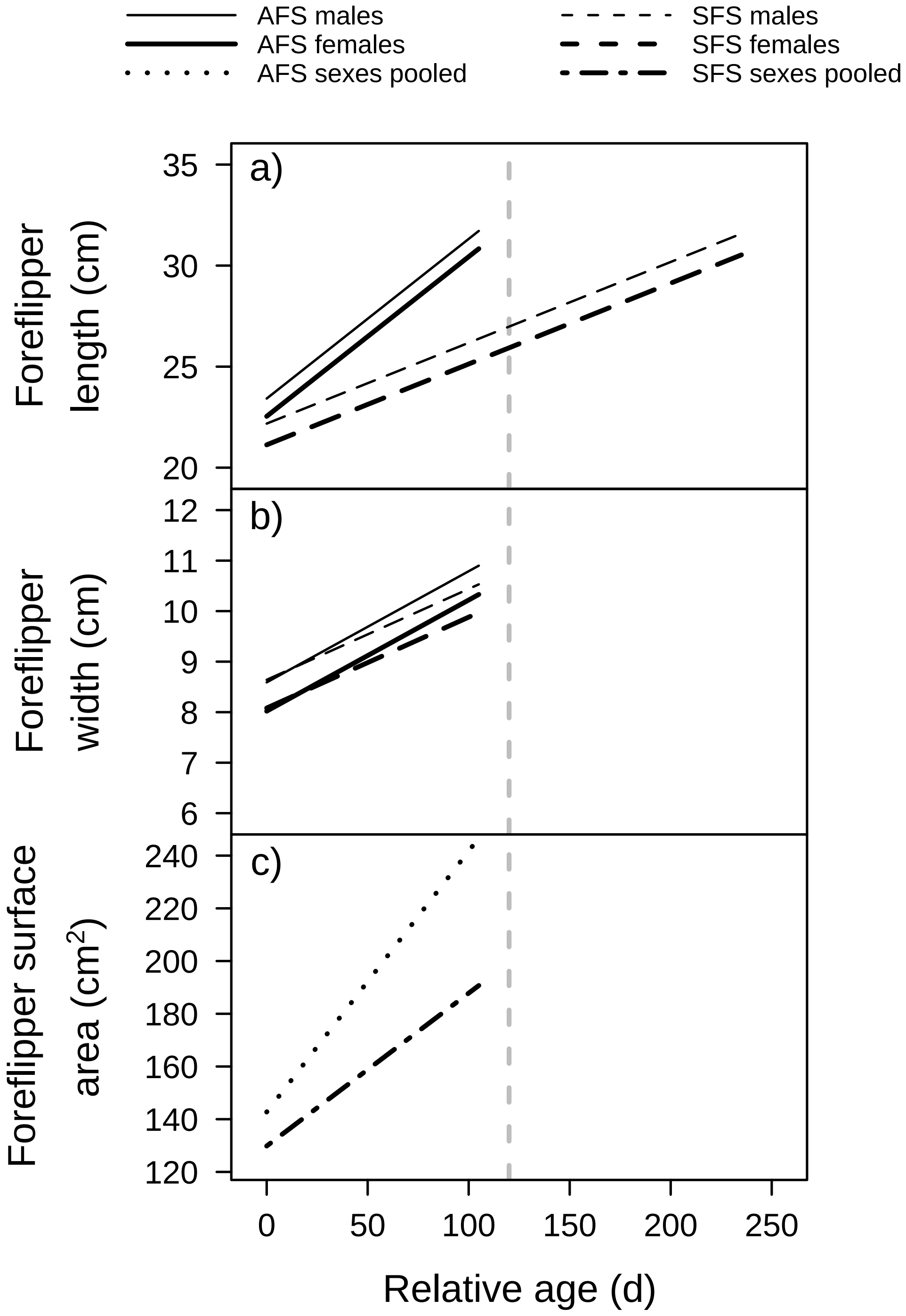

Figure 4.2. Foreflipper length (a), width (b), and surface area (c) grew faster in Antarctic (AFS) compared to subantarctic (SFS) fur seal pups during lactation, based on equation (4.1). The vertical dotted line indicates weaning age of AFS pups. See Table 4.5 for estimated growth rates

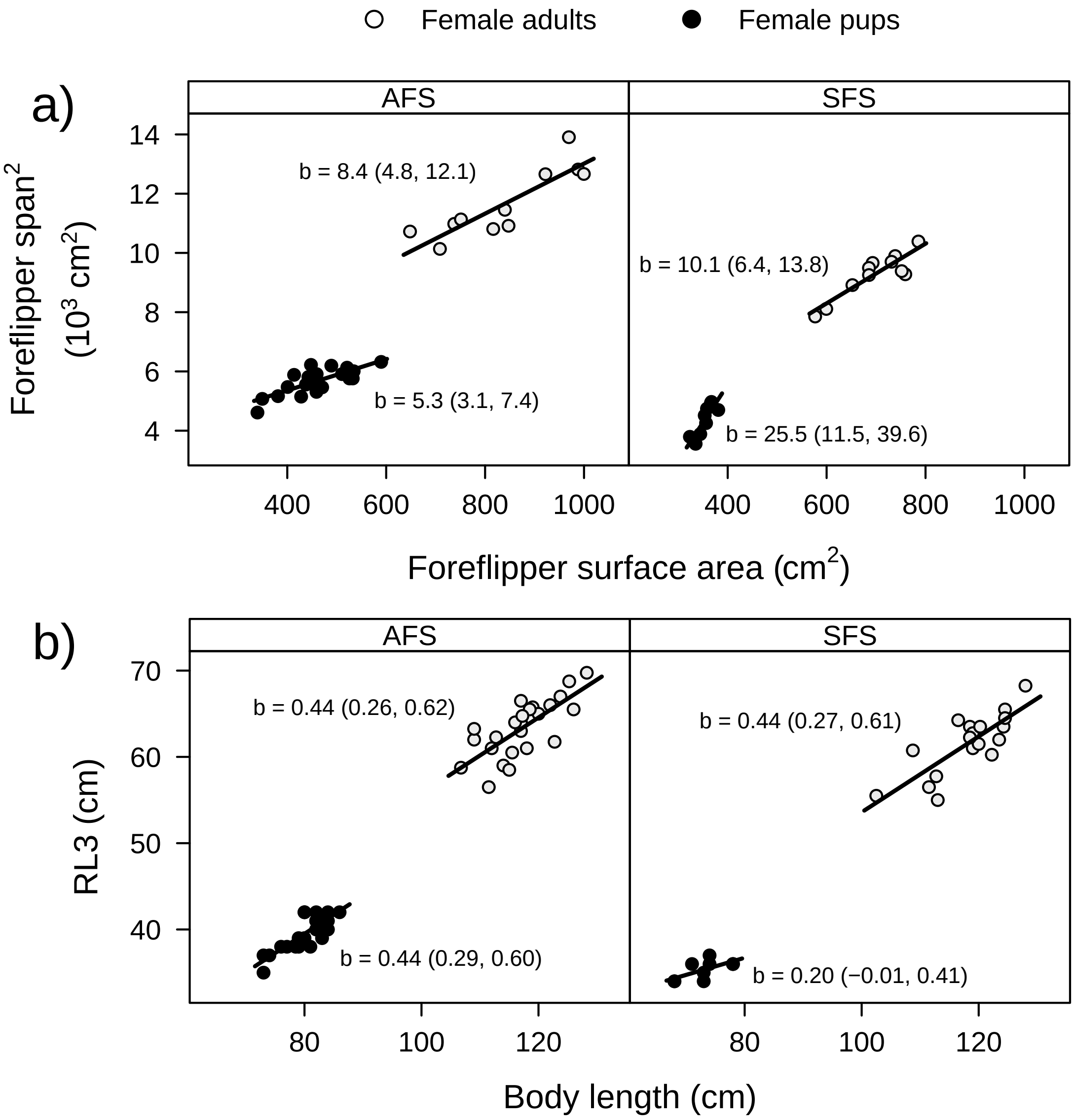

Figure 4.3. Body shape of pups at approximately 100 d of age shows more similarities with that of adults in Antarctic (AFS) than in subantarctic (SFS) fur seals, based on a) aspect ratio (relationship between foreflipper span^2 to foreflipper surface area), and b) relationship of distance distance from tip of nose to axillae (RL3) to body length. The slope of the relationship (lower, upper 95% confidence limits) are shown

Ontogeny of body size and shape of Antarctic and subantarctic fur seals

Sebastián P. Luque, Edward H. Miller, John P.Y. Arnould, Magaly Chambellant, and Christophe Guinet

Abstract: Pre- and post-weaning functional demands on body size and shape of mammals are often in conflict, especially in species where weaning involves a change of habitat. Compared with long lactations, brief lactations are expected to be associated with fast rates of development and attainment of adult traits. We describe allometry and growth for several morphological traits in two closely related fur seal species with large differences in lactation duration at a sympatric site. Longitudinal data were collected from Antarctic (*Arctocephalus gazella* (Peters, 1875); 120 d lactation) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872); 300 d lactation) fur seals. Body mass was similar in neonates of both species, but *A. gazella* neonates were longer, less voluminous, and had larger foreflippers. The species were similar in rate of preweaning growth in body mass, but growth rates of linear variables were faster for *A. gazella* pups. Consequently, neonatal differences in body shape increased over lactation, and *A. gazella* pups approached adult body shape faster than did *A. tropicalis* pups. Our results indicate that preweaning growth is associated with significant changes in body shape, involving the acquisition of a longer, more slender body with larger foreflippers in *A. gazella*. These differences suggest that *A. gazella* pups are physically more mature at approximately 100 d of age (close to weaning age) than *A. tropicalis* pups of the same age.

Résumé : Il y a souvent un conflit entre les demandes fonctionnelles d'avant et d'après le sevrage sur la taille et la forme corporelles chez les mammifères, particulièrement chez les espèces chez lesquelles le sevrage implique un changement d'habitat. Contrairement aux allaitements prolongés, on s'attend à ce que les allaitements courts soient associés à des taux rapides de développement et d'acquisition des caractéristiques adultes. Nous décrivons l'allométrie et la croissance de plusieurs variables morphologiques chez deux espèces fortement apparentées d'otaries à fourrure vivant dans un même site, mais possédant des périodes d'allaitement de durée différente. Nous avons récolté des données longitudinales sur des otaries à fourrure antarctiques (*Arctocephalus gazella* (Peters, 1875); allaitement de 120 j) et subantarctiques (*Arctocephalus tropicalis* (Gray, 1872); allaitement de 300 j). La masse corporelle est semblable chez les nouveau-nés des deux espèces, mais les nouveau-nés d'*A. gazella* sont plus longs et moins volumineux et ils possèdent des nageoires antérieures plus grandes. Les taux de croissance de la masse corporelle avant le sevrage sont similaires chez les deux espèces, mais les taux de croissance des variables linéaires sont plus rapides chez les petits d'*A. gazella*. En conséquence, les différences de forme corporelle à la naissance augmentent au cours de l'allaitement et les petits d'*A. gazella* acquièrent la forme adulte plus rapidement que les petits d'*A. tropicalis*. Nos résultats indiquent que la croissance avant le sevrage est associée à une importante modification de la forme corporelle, ce qui se traduit chez *A. gazella* par l'acquisition d'un corps plus long et plus élancé avec des nageoires antérieures plus grandes. Ces différences laissent croire que les petits d'*A. gazella* âgés d'environ 100 j (près de l'âge de sevrage) ont une maturité physique plus grande que les petits d'*A. tropicalis* du même âge.

[Traduit par la Rédaction]

Introduction

Magnitude, rate, and pattern of mammalian growth determine adult body size and shape (Brody 1964; McNab 2002). Adult body size and shape, in turn, have major influences on viability and reproduction, among other life-history traits (Stearns 1992; Arendt 1997; Lindström 1999). Growth must be optimized relative to other demands, therefore it varies across individuals, populations, and species (Mangel and Stamps 2001; Caley and Schwarzkopf 2004). Some trade-offs occur in offspring, while others are imposed by different trade-offs acting on their mothers, which may alter the quality and quantity of milk that the mothers deliver. Interspecifically, milk composition and energy content are related to duration of lactation, so differences in the latter do not necessarily reflect total energy transferred to the offspring. Tilden and Oftedal (1997) noted that the energy den-

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sity of milk is inversely related to duration of lactation in primates. Similarly, slowly growing and highly mobile offspring typify ungulate and macropod (kangaroos, wallabies, etc.) species with long lactations (Sæther and Gordon 1994; Fisher et al. 2002). However, body size is an important complicating factor, as lactation typically lasts longer in larger species (Peters et al. 1983; Clutton-Brock 1991; Ross 1998). Because of these confounding factors, reasons for interspecific variation in growth with respect to lactation duration remain poorly understood.

Pinnipeds are an attractive model for studying preweaning development because they undergo a transition from suckling on land to foraging at sea, involving major physical, physiological, and behavioural changes in preparation for that transition. The success of the transition ultimately depends on the acquisition of sufficient oxygen stores in relation to energy expenditure while diving (Burns and Castellini 1996; Burns 1999; Thorson et al. 1994; Horning and Trillmich 1997*a*, 1997*b*). However, increased physiological diving capacity must be closely coordinated with physical growth and the gradual development of swimming skills (Jørgensen et al. 2001; Bowen et al. 1999). Recent studies suggest that oxygen storage capacity across a broad range of marine mammal species does not reach adult levels before independent foraging (Noren et al. 2001; Burns et al. 2004). Therefore, lactation duration is an important factor affecting the ontogeny of physical and behavioural traits of offspring.

Relationships between life-history traits have been extensively studied in pinnipeds because they are ecologically and reproductively diverse and display a wide range of body sizes (Stirling and Kleiman 1983; Bonner 1984; Oftedal et al. 1987; Costa 1993; McLaren 1993; Boyd 1998). For instance, lactation lasts from <4 d (hooded seal, *Cystophora cristata* (Erxleben, 1777)) to 2–3 years (walrus, *Odobenus rosmarus* (L., 1758)). Quality of knowledge, however, varies across species; good estimates of lactation duration are available for only eight species — three otariids and five phocids (Schulz 2004). Good quantitative estimates of growth rate and duration of lactation for the same species are available for even fewer. Considering the difficulty in obtaining comprehensive and precise data, and given the widespread effects of spatiotemporal environmental variability on one-time estimates (Trillmich et al. 1991; Lunn et al. 1993), an alternative approach for comparing ecologically different and related species might be profitable. Two otariid species that have recently been used in the context of foraging and growth studies are the Antarctic (*Arctocephalus gazella* (Peters, 1875); AFS hereinafter) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872); SFS hereinafter) fur seals (Kerley 1985; Goldsworthy et al. 1997; Klages and Bester 1998; Goldsworthy and Crowley 1999; Robinson et al. 2002).

We investigated comparative growth in AFS and SFS pups to determine the presence and nature of differences that may influence how the species cope with the critical postweaning period as pups become independent foragers. These species have similar adult body mass and length (Payne 1979; Bester and Van Jaarsveld 1994), yet exhibit a large disparity in lactation duration: 116 d in AFS (Costa et al. 1988; Lunn et al. 1993) and 300 d in SFS (Kerley 1987; Guinet and Georges 2000), respectively. Therefore, the time required to acquire the physical and physiological characteristics enabling pups to become independent foragers may differ between the species. Comparisons between two species cannot be used to elucidate the relationship between lactation duration and growth patterns, but they offer an advantage that is rarely found in multispecies comparisons — the ability to control for confounding factors, such as environmental differences between populations of different species, in syntopic (locally sympatric) populations. AFS and SFS breed syntopically at a few locations where habitat differences between species are likely to be minimal, facilitating the interpretation of comparative analyses.

In previous research, Arnould et al. (2003) found that daily pup energy expenditure was higher in AFS than in SFS breeding syntopically at Ile de la Possession, Crozet archipelago, in the Southern Indian Ocean. In contrast, earlier reports from other syntopic sites suggested higher growth rates in body mass of AFS (Kerley 1985; Goldsworthy and Crowley 1999). We suggest that the reported disparity may reflect differences in body shape, which commonly differs adaptively between related species (Dodson 1975; Carrier 1983; Alatalo et al. 1984; Atchley 1984; Creighton and Strauss 1986; Gisbert 1999; Hochuli 2001).

Functional demands on body size and shape may change sharply between pre- and post-weaning ages in young pinnipeds, especially in otariids because of their long preweaning terrestrial existence (Koehler and Barclay 2000). Within the otariids, AFS and SFS differ substantially in this regard, so we predicted that these species would differ in growth trajectories and in the rate at which they acquire adult body form or shape (e.g., in foreflippers; Fish 1998; Fish et al. 2003). Specifically, we predicted that AFS pups should acquire adult flipper size and shape relatively sooner than would SFS pups, assuming that this allows them to make a successful transition to independent foraging at an earlier age.

Materials and methods

Fur seal colonies and identification procedures

Research was carried out at La Mare aux Elephants (46°22′29″S, 51°40′13″E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001–2002 (4 December – 25 March) and 2002–2003 (1 December – 16 March) breeding seasons (2001 and 2002 hereinafter). The site consists of two adjacent AFS and SFS colonies on different types of substrate — AFS on the northern part of the beach, which is composed of small to medium-sized pebbles, with gentle slopes behind; SFS on the southern part of the beach, which is composed of large boulders that have fallen from the steep hinterlands. Both species give birth close to shore, but the AFS colony grows in size as the season progresses, while the other species tends to remain close to shore during the same period.

Pups were individually marked (Georges and Guinet 2000; Arnould et al. 2003; Bailleul et al. 2005) over a 6 d (2001) or 13 d (2002) period (Table 1). Pup production and mean pupping date were estimated using (*i*) total pup counts (both years; including dead and living pups) on a weekly ba-

Table 1. Summary of numbers of Antarctic (*Arctocephalus gazella*; AFS) and subantarctic (*Arctocephalus tropicalis*; SFS) fur seal used in the study, broken down by year, species, and sex.

	Breeding season		
	2001	2002	Both
AFS			
Female	47 (10)	29 (24)	76
Male	48 (6)	29 (19)	77
Both	95	58	153
SFS			
Female	31 (27)	36 (32)	67
Male	27 (22)	30 (28)	57
Both	58	66	124

Note: Values indicate total number, including newborn pups; the number of newborn pups is shown in parentheses.

sis until no more births were observed and (*ii*) mark–recapture methods (2001 only). Peak pupping dates were 5 and 15 December (2001: 164 pups; 2002: 167 pups) for AFS, and 25 and 30 December (2001: 80 pups; 2002: 91 pups) for SFS. Populations of both species have been increasing at an annual rate of approximately 18% annually at least until 1994 (Guinet et al. 1994).

Morphometric measurements

Body mass (BM) of pups was measured to the nearest 0.05 at first capture, and every 5–9 d thereafter, on a 25 kg capacity digital suspension balance (ElectroSamson; Salter Brecknell, Fairmount, Minnesota). The following variables were also measured on pups upon first capture and every 12–16 d thereafter: body length (BL; nearest 0.5 cm, straight line from the tip of the nose to the flesh tip of the tail) with a tape measure, while animals were manually restrained over a board and positioned straight and flat on their ventral surface. In 2002, we also measured the following variables (nearest 0.5 cm) taken the same way and on the same schedule: body girth at levels of pinna, mid-neck, axillae, and umbilicus (G1–G4 hereinafter); distance from the tip of the nose to each of these points (see next; RL1–RL4 hereinafter). BL and RL1–RL4 were measured with a straight tape measure glued onto the board on which the animals were placed. Length, width, and surface area of foreflippers were measured as follows. First, the right foreflipper was extended and held to the side of and perpendicular to the body, and was placed on a wooden board with horizontal and vertical scales (20 cm, marked every 5 cm). Second, a photograph was taken (Nikon Coolpix E885) in dorsal aspect from a distance of approximately 1.25 m. Finally, measurements were made from the photographs: (*i*) length (FL), defined as the distance from proximal end of the humerus (estimated by palpation) to the tip of foreflipper through the midline of the flipper; (*ii*) width (FW), defined as the largest distance perpendicular to the foreflipper length; and (*iii*) area (FA), estimated from the traced outline of the foreflipper using Object-Image version 2.11 (US National Institutes of Health, available from http://simon.bio.uva.nl/Object-Image/object-image.html [accessed 12 December 2007]). FL and FW were also measured directly on the foreflipper for cross-validation and subsequent analyses.

The relationship between direct measurements on flippers, and those taken photogrammetrically, were tested for linearity to detect outliers or invalid estimates. This led to the exclusion of FA estimates for pups with FL >27 cm, as the corresponding relationship became asymptotic beyond this value, indicating decreasing accuracy.

We also took all measurements on 63 AFS and 70 SFS adult females, but BM was measured to the nearest 0.5 kg. For comparisons with pups, each female was measured at least twice, and the median value for each variable was used to set adult body measurements. Estimates for some variables on adult males were included using data taken at South Georgia for AFS (Payne 1979) and at Marion Island (about 950 km west of Crozet) for SFS (Bester and Van Jaarsveld 1994).

Body volume (BV; ±0.01 L) of pups was obtained by using model B in Luque and Aurioles-Gamboa (2001), in which the body was modelled as two cones plus two truncated cones. Volumes of cones ($\frac{1}{3}\pi h(r_1^2 r_2^2 + r_1^2 r_2^2)$) and truncated cones ($\frac{1}{3}(\pi r^2 h)$) were calculated using the lengths (h) of cones estimated from RL1 and RL4, and lengths of truncated cones were estimated from RL2 and RL3, respectively. Girth was used to calculate radius (r).

Analyses

Interspecific differences in neonatal and adult body size were assessed using double classification analyses of variance, with a term for sex effects, including only data for which accurate ages were available. However, adult females were assigned to a single age category because their ages were unknown.

To determine whether growth trajectories varied according to species or sex, a linear mixed effects model (Raudenbush and Bryk 2002) was designed for the jth observation on the ith individual:

$$[1] \qquad y_{ij} = (\beta_{00} + \beta_{01}\mathrm{species}_i + \beta_{02}\mathrm{sex}_i + \beta_{03}\mathrm{species}_i\mathrm{sex}_i + b_{i0}) + (\beta_{10} + \beta_{11}\mathrm{species}_i + \beta_{12}\mathrm{sex}_i + \beta_{13}\mathrm{species}_i\mathrm{sex}_i + b_{i1})x_{ij} + \varepsilon_{ij}$$

where β_{00} and β_{10} refer to the population intercept and slope, respectively, for AFS female pups, which is the baseline group. β_{01}, β_{02}, and β_{03} are fixed effects for the change in population intercept associated with the species, sex, and their interaction in relation to the baseline group. β_{11}, β_{12}, and β_{13} are the changes in population slope associated with the same effects. b_{i0} and b_{i1} are the random intercept and slope effects for the ith individual, respectively, and ε_{ij} is a within-subject residual term. Other terms were added to test for year effects and their interactions with body mass and body length, but they were subsequently dropped if they were nonsignificant here and elsewhere at $\alpha = 0.05$.

Based on exploratory analyses and because ages were <300 d, a linear model was assumed, rather than a more complicated one. No assumptions were made regarding the autocorrelation structure of the ε_{ij} values. However, it was assumed that these were independent and normally distributed, regardless of the b_i values. In this model, species$_i$ and sex$_i$ take on values of zero and one, to indicate whether y_{ij} refers to AFS or SFS, and to a female or a male pup, respectively. We fitted the model using a restricted log-likelihood method, as described in Pinheiro and Bates (2000), and implemented in the NLME R package (Pinheiro et al. 2004). We subsequently estimated linear equations from this model, collapsing across and (or) within fixed effects that were not significantly different from zero. Only pups that were measured more than twice throughout the study period were considered for these analyses.

Because absolute age was not known for all individuals (Table 1), relative age was defined as the number of days elapsed since seals were first seen, which was taken as day zero. The difference in peak pupping dates between species was taken into account by adding the corresponding value from each breeding season (2001: 20 d; 2002: 15 d) to the relative age of AFS pups. Relative age was then used as the regressor x in eq. 1. Relative age was logarithmically transformed (logarithm base 10) and a constant was added to it to achieve linearity before using it as the regressor for BL in eq. 1. This transformation was chosen because BL changed faster in young pups (<30 d) than in older pups.

To address the question of whether growth trajectories gave rise to interspecific differences in the rate at which pups acquired adult body shape, two allometric relationships that might influence aquatic locomotory performance (e.g., Feldkamp 1987; Fish et al. 1988; Stelle et al. 2000) were studied: (1) foreflipper span (FS) squared vs. total FA (TFA) and RL3 vs. BL. FS was calculated as $2 \cdot \mathrm{FL} + \mathrm{G3} \cdot \pi^{-1}$ and TFA was calculated as $2 \cdot \mathrm{FA}$. The first relationship is the foreflipper aspect ratio expressed allometrically, whereas the second was used as an index of the position of foreflippers along the body axis relative to BL. One random measurement per female pup, where 80 d < age < 120 d, was selected for this analysis to eliminate any dependence between observations while maintaining a large enough sample size with valid foreflipper measurements (i.e., <27 cm). For adult females, the median value for each variable was used, assuming their growth was negligible.

To investigate how allometric relationships 1 and 2 compared between species and age groups (female pups vs. adult females), we used analysis of covariance (Zar 1996). We were interested in the interaction between age group (adult or pup) and species to test whether pups of one species were more allometrically similar to adults than the other. This approach avoided known biases associated with ratios between the variables from each relationship (Packard and Boardman 1999).

All statistical analyses were performed in the GNU R system (R Development Core Team 2006). The Shapiro–Wilks statistic and the Fligner–Killeen test were used to evaluate assumptions of normality of data distributions and homogeneity of variances, respectively, in analyses of variance and covariance. Results show SE as the measure of dispersion, unless stated otherwise.

Results

Neonatal and adult body size

There was no evidence of interannual effects on neonatal BM ($F_{[1,160]} = 1.70$, $P = 0.19$) or body length ($F_{[1,157]} = 2.03$, $P = 0.16$) when species and sex were taken into account. Therefore, measurements were pooled across years for subsequent analyses.

Male neonates were larger than females in most measurements (Table 2). AFS neonates were significantly longer than SFS neonates, had longer head and neck regions (RL1 and RL2), longer and narrower foreflippers, and greater FA (Table 2). Other interspecific differences were detected among females only; AFS female pups were larger in girth and BV than SFS pups. Adult female AFS were significantly heavier than adult female SFS. AFS adult females were larger in all flipper measurements than SFS adult females (Table 3).

Growth

Growth trajectories for each variable showed differing patterns of growth between species. No main effects or interactions of year with species or sex effects were significant in the models of mass and body length growth ($P > 0.5$, all cases), so the data were pooled. The magnitude and SE of interspecific and intersexual effects, in terms of eq. 1, are shown in Table 4. Estimated growth rates for each variable, with results of interspecific comparisons, are shown in Table 5.

In both species, sexual differences in BM increased steadily throughout lactation owing to the faster growth of male pups ($t_{[2822]} = 4.0$, $P < 0.01$). However, pups grew at a similar rate in both species ($t_{[2822]} = -0.04$, $P > 0.90$) after the sex effects were removed (Fig. 1). Neonatal BM did not differ between species, but the intercept of the relationship between BM and relative age was higher in AFS pups. No interactions were significant between species ($t_{[264]} = -1.34$, $P > 0.1$) and sex (; $t_{[2822]} = 0.18$, $P > 0.8$). A similar pattern was found for BV (Fig. 1), which is consistent with faster rates of growth in SFS girth (Table 5).

Growth in BL was faster in AFS pups ($t_{[1321]} = -2.57$, $P = 0.01$), as well as in males of both species ($t_{[1321]} = 2.21$, $P = 0.03$) (Fig. 1). There were no interactions between species and sex for slope ($t_{[1321]} = -0.05$, $P > 0.9$) or intercept ($t_{[260]} = -0.93$, $P > 0.3$). RL1 and RL2 showed faster rates of growth in AFS ($t_{[441]} = -4.65$, $P < 0.01$ and $t_{[441]} = -2.80$, $P < 0.01$, respectively), irrespective of sex ($t_{[441]} = 1.49$, $P > 0.1$ and $t_{[441]} = 1.53$, $P > 0.1$, respectively) (Table 5).

All foreflipper measurements increased in size faster in AFS: FL ($t_{[441]} = -10.50$, $P < 0.02$), FW ($t_{[441]}$ -2.45, $P < 0.02$), and FA ($t_{[208]} = -5.13$, $P < 0.01$) (Fig. 2). There were no significant interactions with sex (FL: $t_{[441]} = 0.96$, $P > 0.3$; FW: $t_{[441]} = 1.92$, $P > 0.3$; FA: $t_{[208]} = 0.47$, $P > 0.6$).

Allometry

Pup growth trajectories along individual variables led to differing allometric relationships between species and age

Table 2. Summary of morphometric differences between species and sexes in neonatal Antarctic (AFS) and subantarctic (SFS) fur seals.

	Female		Male		
Variable	AFS	SFS	AFS	SFS	*F* ratio[a]
Body mass (BM; kg)	4.90±0.150	4.60±0.080	5.40±0.210	5.45±0.100	0.98; **35.28**
Body length (BL; cm)	60.3±0.54	58.8±0.32	63.8±0.75	61.7±0.40	**11.34**; **46.63**
Girth (G; cm)					
G1	30.4±0.30[b]	28.9±0.14	30.6±0.26	30.4±0.15	**9.57**
G2	29.5±0.32[b]	27.4±0.26	28.6±0.48	29.2±0.27	**16.22**
G3	39.6±0.54[b]	37.2±0.33	39.3±0.71	39.6±0.43	**7.87**
G4	39.1±0.64[b]	36.7±0.41	39.1±0.72	40.2±0.55	**9.27**
Reference length (RL; cm)					
RL1	8.3±0.13	7.8±0.11	8.8±0.17	8.1±0.11	**25.33**; **9.24**
RL2	12.9±0.15	12.1±0.16	13.6±0.30	12.8±0.19	**16.86**; **14.16**
RL3	30.3±0.41	29.0±0.37	31.1±0.62	30.9±0.43	2.45; **11.15**
RL4	43.8±0.43	40.2±0.34	45.0±0.59	41.9±0.37	**62.84**; **13.99**
Foreflipper length (FL; cm)	22.2±0.23	21.1±0.14	23.0±0.45	22.0±0.18	**21.66**; **13.77**
Foreflipper width (FW; cm)	8.0±0.11	8.2±0.10	8.4±0.17	8.8±0.10	**10.95**; **24.10**
Foreflipper surface area (FA; cm^2)	142.1±3.57[b]	126.6±2.41	145.4±5.99	144.1±2.50	**4.30**
Body volume (BV; L)	4.5±0.15[b]	3.6±0.08	4.5±0.21	4.2±0.11	**4.93**

Note: For all variables, sample sizes (*n*) were 22 females and 17 males (AFS) and 32 females and 28 males (SFS), except for body mass and body length, where the sample sizes were 34 females and 25 males (AFS) and 59 females and 50 males (SFS). Values are means ± SE.

[a] Values for interspecific and intersexual comparisons, respectively, are shown. Significant effects are in boldface type. For significant interactions, only the value for the interaction is shown.

[b] For significant interactions, this is the species and sex with the highest mean.

Table 3. Summary of morphometric differences between adult Antarctic (AFS) and subantarctic (SFS) fur seal females.

Variable	AFS	SFS	*F* ratio[a]
Body mass (BM; kg)	32.7±0.36 (63)	30.5±0.45 (70)	**6.88**
Body length (BL; cm)	118.0±0.49 (63)	117.0±0.51 (70)	1.07
Axillary girth (G3; cm)	75.0±0.70 (24)	73.8±1.12 (22)	0.44
Reference length (RL3; cm)	63.3±0.52 (24)	61.6±0.55 (18)	2.74
Foreflipper length (FL; cm)	40.3±0.25 (62)	33.9±0.23 (70)	**179.80**
Foreflipper width (FW; cm)	12.9±0.08 (62)	11.9±0.07 (70)	**43.8**
Foreflipper surface area (FA; cm^2)	431.5±11.46 (16)	348.1±6.4 (11)	**17.67**

Note: Values are means ± SE, with sample size (*n*) in parentheses.

[a] Significant effects are in boldface type.

groups. A two-way analysis of covariance indicated that age-group differences in the slope of the relationship between FS^2 and TFA were dependent on species (slope interaction term: $F_{[1,43]} = 5.00$, $P = 0.03$). The age group did not significantly affect the allometric slope in AFS ($F_{[1,27]} = 2.83$, $P = 0.10$), but it did in SFS ($F_{[1,16]} = 5.29$, $P = 0.04$); female SFS pups had a higher allometric slope than adult females (Fig. 3A). Among pups, the allometric slope showed large differences between species ($F_{[1,25]} = 11.4$, $P = 0.002$), but it was similar between species among adults ($F_{[1,18]} = 0.36$, $P = 0.55$). In agreement with this trend, differences in the allometric slope between pups and adults were larger in SFS. Foreflipper size differences between pups and adults were also much larger in SFS.

RL3 scaled with BL differently between species ($F_{[1,69]} = 6.01$, $P = 0.02$), but similarly between age groups ($F_{[1,69]} = 0.29$, $P = 0.59$), without any interaction between these factors ($F_{[1,65]} = 1.08$, $P = 0.30$). The allometric slope of the relationship was higher in AFS, particularly among female pups (Fig. 3B).

Discussion

Neonatal and adult body size

Based on multiple traits, we documented many interspecific differences in neonatal body size, preweaning growth, and changes in body growth between two otariid species, AFS and SFS. We hypothesized that AFS pups should mature physically faster than SFS pups, given their younger weaning age. Neonates of the two species differed little on any measurements, but differed greatly in rates of growth. However, if adults show larger differences between species than neonates, then the results may simply reflect intrinsic morphological differences between species rather than different development patterns. Therefore, we begin our discussion by comparing neonate and adult body size of AFS and

Table 4. Summary of the effects of species (β_{01} and β_{11}), sex (β_{02} and β_{12}), and their interactions (β_{03}) on the growth of Antarctic and subantarctic fur seal pups, estimated using eq. 1.

	Intercept effect			Slope effect	
Variable	β_{01}	β_{02}	β_{03}	β_{11}	β_{12}
Body mass (BM)	**–0.950 (0.180)**		ns	ns	**0.010 (0.003)**
Body length (BL)[a]			ns	**–1.740 (0.680)**	**1.410 (0.640)**
Foreflipper length (FL)		**0.880 (0.330)**	ns	**–0.040 (0.004)**	ns
Foreflipper width (FW)	ns	**0.570 (0.140)**	ns	**–0.004 (0.001)**	ns
Foreflipper surface area (FA)		ns	ns	**–0.410 (0.080)**	ns
Body volume (BV)	**–1.030 (0.230)**		ns	ns	**0.010 (0.004)**
Girth (G)					
G1	**–1.400 (0.300)**	**0.860 (0.310)**	ns	ns	ns
G2		ns	**1.700 (0.750)**	**0.040 (0.008)**	ns
G3		ns	ns	**0.030 (0.010)**	ns
G4		ns	ns	**0.060 (0.015)**	ns
Reference length (RL)					
RL1		**0.550 (0.190)**	ns	**–0.010 (0.003)**	ns
RL2		**1.150 (0.310)**	ns	**–0.020 (0.006)**	ns
RL3	**–2.770 (0.580)**	**1.530 (0.590)**	ns	ns	ns
RL4	**–4.070 (0.590)**		ns	ns	ns

Note: The interactions in slope β_{13} were nonsignificant, therefore they were omitted. Significant effects are in boldface type; nonsignificant effects are indicated by ns; meaningless effects owing to interactions are blank. Standard errors are in parentheses.

[a] Relative age (d) was log-transformed to linearize this relationship.

Table 5. Comparison of growth rates of Antarctic (AFS) and subantarctic (SFS) fur seal pups, using the estimated slope (lower–upper 95% confidence limits) from eq. 1.

	Female		Male	
Variable	AFS	SFS	AFS	SFS
Body mass (BM; kg·d^{-1})	0.06 (0.06–0.07)[a]		0.08 (0.07–0.08)[a]	
Body length (BL; cm·log(d^{-1}))	17.58 (16.68–18.47)	15.83 (14.85–16.82)	18.99 (18.11–19.86)	17.19 (16.15–18.23)
Girth (G; cm·d^{-1})				
G1	0.04 (0.04–0.05)[b]			
G2	0.07 (0.06–0.08)	0.10 (0.09–0.11)	0.09 (0.07–0.10)	0.10 (0.09–0.1)
G3	0.14 (0.13–0.15)	0.17 (0.15–0.18)	0.14 (0.13–0.15)	0.17 (0.15–0.18)
G4	0.09 (0.08–0.11)	0.15 (0.13–0.18)	0.09 (0.08–0.11)	0.15 (0.13–0.18)
Reference length (RL; cm·d^{-1})				
RL1	0.05 (0.05–0.06)	0.04 (0.03–0.04)	0.05 (0.05–0.06)	0.04 (0.03–0.04)
RL2	0.10 (0.10–0.11)	0.09 (0.08–0.10)	0.10 (0.10–0.11)	0.09 (0.08–0.10)
RL3	0.10 (0.09–0.11)[b]			
RL4	0.13 (0.13–0.14)[b]			
Foreflipper length (FL; cm·d^{-1})	0.08 (0.08–0.08)	0.04 (0.03–0.05)	0.08 (0.08–0.08)	0.04 (0.03–0.05)
Foreflipper width (FW; cm·d^{-1})	0.02 (0.02–0.02)	0.02 (0.02–0.02)	0.02 (0.02–0.02)	0.02 (0.02–0.02)
Foreflipper surface area (FA; cm·d^{-1})	0.99 (0.89–1.09)	0.58 (0.45–0.72)	0.99 (0.89–1.09)	0.58 (0.45–0.72)
Body volume (BV; L·d^{-1})	0.04 (0.03–0.04)[a]		0.04 (0.04–0.05)[a]	

[a] Growth rate was common to both species.

[b] Growth rate was common to both species and both sexes.

SFS at Iles Crozet with other populations, and then focus on the factors that could have given rise to species differences in development.

We found no species differences in neonatal body mass at Iles Crozet, as Kerley (1985) also found for seven animals at Marion Island. No comparable data are available from Macquarie Island, the third site where the two species coexist. However, body mass alone cannot be used to compare body size between the species, because neonatal body shape differs — at birth, AFS pups are longer, have longer heads and necks, and have larger foreflippers. Therefore, the similarity between species in body mass may indicate differences in body composition rather than similarities in body size. Based on a small sample of our pups from 2001, Arnould et al. (2003) showed that AFS pups had lower total body lipid stores than SFS pups at approximately 2 months of age, and our results suggest that the difference may also be present at birth.

Neonates of both species from our study were about a kilogram heavier than those weighed by Sparrow and Heywood (1996), although the difference cannot readily be attributed to any ecological factor because of the small

Fig. 1. Rates of growth in body mass (A) and body volume (B) did not differ between Antarctic (*Arctocephalus gazella*; AFS) and subantarctic (*Arctocephalus tropicalis*; SFS) fur seal pups during lactation, but growth in body length (C) was faster in AFS pups, based on eq. 1. The vertical broken line indicates weaning age of AFS pups. See Table 5 for estimated growth rates.

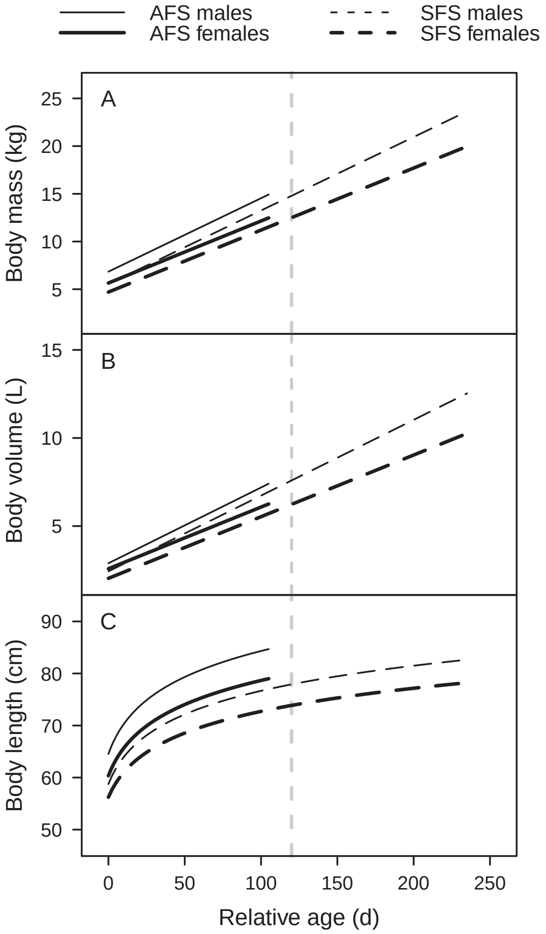
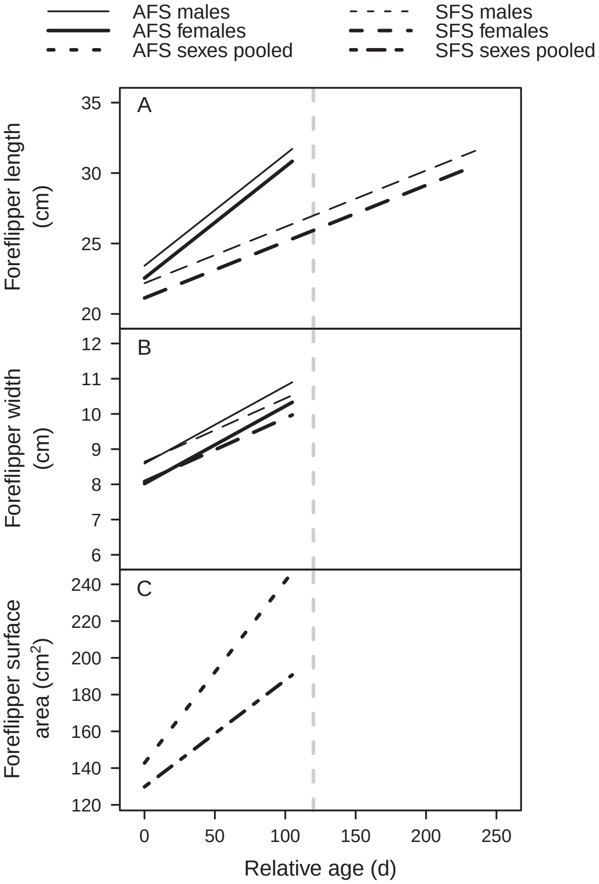


Fig. 2. Foreflipper length (A), width (B), and surface area (C) grew faster in Antarctic (AFS) compared with subantarctic (SFS) fur seal pups during lactation, based on eq. 1. The vertical broken line indicates weaning age of AFS pups. See Table 5 for estimated growth rates.

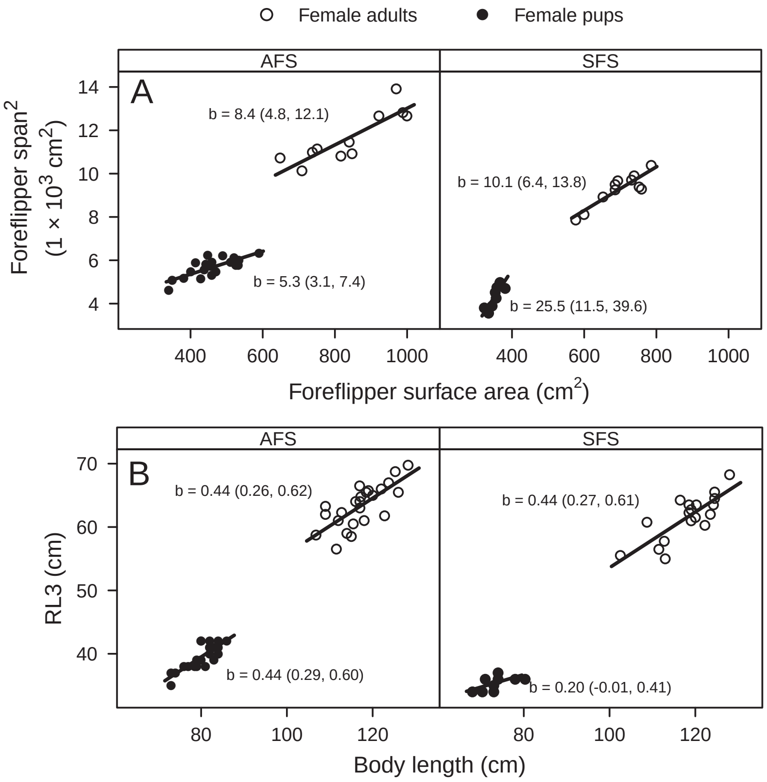


sample size in the latter study. Estimated pup birth dates in our study were similar to those reported by Kerley (1985) on Marion Island and were consistent with Sparrow and Heywood (1996), who showed that the two archipelagoes have a similar marine environment. The body mass of neonatal SFS pups in our study is comparable with that obtained from allopatric sites at Amsterdam Island (Georges and Guinet 2000) and Gough Island (Bester 1987; Bester and Van Jaarsveld 1994) for SFS and at Bird Island, South Georgia (Lunn et al. 1993), for AFS, suggesting that adult females are equally able to meet the demands of gestation in these environments, or can compensate for any differences without a cost to the newborn offspring.

Sexual differences in neonatal body size occur in all otariids, including in our species (Bester 1987; Kerley 1985; Lunn et al. 1993). However, pup sex did not influence most interspecific comparisons of neonatal body size in our analyses; sexual size differences were similar for both species, except for girth measurements, body volume, and foreflipper surface area. For the latter three variables, AFS pups were larger than their congenerics only among females. The larger axillary girth and body volume of female AFS pups may reflect sex-specific differences in relative body lipid stores. Several authors have reported higher total body lipid stores in female pups compared with male pups belonging to several species (e.g., Arnould et al. 1996; Donohue et al. 2002; Beauplet et al. 2003), including those in this study. Therefore, everything else being equal, female pups would be expected to be more voluminous than male pups (Luque and Aurioles-Gamboa 2002).

Intraspecifically in pinnipeds, large mothers tend to give birth to large pups (Costa et al. 1988; Arnbom et al. 1997; Mellish et al. 1999). Boltnev and York (2001) found that neonatal mass increases at a decelerating rate with maternal mass in northern fur seals (*Callorhinus ursinus* (L., 1758)). The same relationship appears to hold interspecifically (Costa 1991), but whether the relationship is linear or not is unclear. Adult female AFS did not give birth to heavier pups in our study, despite being heavier than adult female SFS.

Fig. 3. Body shape of pups at approximately 100 d of age shows more similarities with that of adults in Antarctic (AFS) than in subantarctic (SFS) fur seals, based on (A) aspect ratio (relationship between foreflipper span^2 to foreflipper surface area) and (B) relationship between distance from tip of nose to axillae (RL3) and body length. The slopes (*b*) of the relationship (lower, upper 95% confidence limits) are shown.



Compared with body mass, linear measurements (body length, axillary girth, and RL3) of physically restrained fur seals include larger measurement errors, reducing the statistical power of interspecific comparisons. Therefore, comparisons of pup body size in relation to maternal body size require more accurate measurements.

Both adult females and neonates differed in body shape between species, so interspecific differences in growth of body size may simply reflect morphological differences between AFS and SFS. We did not measure adult males of both species at La Mare aux Elephants, so we cannot generalize the argument to both sexes. However, if growth rates of individual variables were mainly determined by species-specific morphometric traits, then interspecific differences in these traits would be expected to be similar in neonates and adults, and body shape would be expected to remain relatively constant with age. Both expectations from this argument were not supported by our results. The magnitudes of morphometric differences between species were considerably larger among adult females than among neonates, and more similarities in body shape between adult females and 80–120 d old pups were found in AFS than in SFS. Therefore, the growth patterns exhibited by each species may not be only related to intrinsic morphometric differences between them.

Preweaning growth and allometry

We found no interspecific differences in rate of growth in body mass. This contrasts with previous studies of these species where they are sympatric (Marion Island: Kerley 1985; Macquarie Island: Goldsworthy and Crowley 1999). Our estimates of growth rates in body mass also were lower at Ile de la Possession than at those two sites. The reasons for such discrepancy are not clear, but methodological differences in pup sampling protocol (longitudinal vs. cross-sectional) and period of lactation covered hinder the comparison of results among these studies.

In our study, SFS and AFS pups had similar rates of growth in body mass and body volume. However, AFS pups had (*i*) faster rates of growth in body length, length of anterior portions of the body (RL1–RL2), and foreflipper dimensions, and (*ii*) lower rates of growth in body girth. These differences lead to a more streamlined body with relatively large foreflippers in AFS and a stockier body in SFS.

Two-species comparisons cannot provide general conclusions about relations between lactation duration and growth pattern (Garland and Adolph 1994) in otariids, but by minimizing other confounding factors, such a comparison can provide insights into possible mechanisms (Fisher et al. 2002). We hypothesized that AFS pups would exhibit more precocial growth than SFS pups. In AFS, differences between pup and adult foreflipper shape, as well as their position along the body, differed more than in SFS, which supports this hypothesis. These differences were reflected in the relationship between foreflipper span^2 and foreflipper surface area, which defines an important measure (aspect ratio) of aquatic locomotory ability (e.g., Feldkamp 1987; Fish et al. 1988; Norberg et al. 1993). For instance, low aspect ratio flippers are associated with increased costs of transport during steady swimming, but are better suited for rapid accelerations during quick turns in open water (Fish and Nicastro 2003; Fish et al. 2003). A similar argument can be made for the relationship between RL3 and body length, which is an index of the position of the foreflippers along the body. Relative position of the foreflippers along the body may have functional significance in aquatic stability and maneuverability, which is favoured when foreflippers are located far from the center of gravity (Fish et al. 2003).

Allometric analysis (Figs. 3A, 3B) suggests that AFS pups have foreplippers positioned more posteriorly along the body, as well as lower foreflipper aspect ratio, than SFS pups, and hence potentially greater aquatic turning abilities at 100 d (±20) of age. However, while AFS pups are near the end of lactation at this age, SFS pups are in mid-lactation, so increased aquatic turning abilities may be more critical for the former. Indeed, the largest foreflipper surface areas of female AFS pups were close to adult values, which was not the case for female SFS pups. Further studies are needed to assess the effect of differences in flipper size and structure for terrestrial locomotion, as well as the acquisition of foraging skills at sea, of these two species. Other factors that are likely to influence this process, such as the timing and pattern of moulting, should also be considered because they are known to affect pup thermoregulatory ability (Donohue et al. 2000).

To summarize, we found many differences in growth of AFS and SFS pups at Iles Crozet, where the species breed sympatrically, but maintain species-specific differences in lactation duration. Compared with SFS pups, AFS pups adopted a growth strategy that favours the acquisition of a longer, more slender body with larger foreflippers. The growth differences between species led to different allometric relationships between female pups and adult females, whereby AFS pups showed more similarities in foreflipper shape and position along the body with their adult counterparts than SFS pups. These interspecific comparisons of allometric relationships suggest AFS pups are physically more mature at approximately 100 d of age (close to weaning age) than SFS pups of the same age. Whether SFS pups achieve a similar level of physical maturity close to their weaning age, and whether different morphological development patterns affect the ontogeny of foraging skills, remain to be determined.

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Chapter 5

Pup physiological development and growth dynamics

Abstract

Otariid pinnipeds exhibit large variation in lactation duration, and pups wean at different times of cycles in marine productivity. Therefore, pup growth and development patterns differ between species, intimately associated with maternal care strategies. Interspecific comparisons to understand the mechanisms driving variation in otariid maternal care strategies and pup development are difficult due to the inability to control for confounding effects of differences in environment. I compared the body composition and dynamics of mass changes associated with maternal attendance and foraging trips in two closely related, morphologically similar, fur seal species at a syntopic site. I measured total body lipids, absolute mass gain (milk intake) during maternal attendance, and mass-specific rate of mass loss during maternal foraging trips in Antarctic (*Arctocephalus gazella* Peters 1875; 120 d lactation) and subantarctic (*A. tropicalis* Gray 1872; 300 d lactation) fur seal pups. Relative to body mass, total body lipid stores increased during lactation, and were larger in *A. tropicalis* pups. Absolute mass gain increased with the duration of the preceding maternal foraging trip, but the slope of this relationship was higher for *A. gazella*, so that mass gained per day mothers spent at sea and average mass gain was larger

in this species. Milk fat content increased similarly for both species during lactation, and total energy intake was larger for *A. gazella* pups at any given age. Mass-specific rate of mass loss did not differ between species among females, but female *A. gazella* pups had higher rates of mass loss than their congenerics of the same sex. These results support previous suggestions that maternal expenditure during foraging cycles is larger in *A. gazella*, and that pups of this species are under stronger selection to develop lean body mass, in preparation for weaning at a younger age, at a time of reduced prey availability.

5.1 Introduction

Lactation is the main form of parental care in mammals and the most energetically expensive activity for females (Pond 1977, Gittleman and Thompson 1988). A wide spectrum of physiological and behavioural adaptations allows females to cope with the large energy costs of lactation, under a variety of conditions (Millar 1977, Pond 1977, Prentice and Prentice 1988). Mothers and offspring interact closely during lactation, influencing each other's physiology and behaviour according to their own fitness interests (Trivers 1974, Rogowitz 1996). The process occurs in a context of large variation in the physical environment, giving rise to complex patterns in lactation strategies. In pinnipeds, lactation strategies can be ordered along a continuum ranging from strict "income" to "capital" strategies (Drent and Daan 1980, Boyd 1998), determined primarily by differences in energy storage capabilities relative to body size. However, lactation duration, a major component of lactation strategy, is highly variable even among species at either end of this spectrum (Schulz and Bowen 2005, Trillmich and Weissing 2006). Therefore, characterization of pinniped lactation strategies remains difficult after several decades of research.

According to an early hypothesis (Gentry et al. 1986) to explain latitudinal variation in duration of lactation of otariids (fur seals and sea lions), species breeding at subpolar latitudes [e.g. Antarctic (*Arctocephalus gazella* (Peters, 1875)) and northern (*Callorhinus ursinus* (L., 1758)) fur seals] exhibit brief lactations (4 mo) due to the combination of high seasonality, predictability, and productivity of the environment, compared to species breeding at lower latitudes. In these conditions, lactation is restricted to summer and early fall, when prey availability is highest and close to the colony. At the other extreme, otariids breeding in the tropics [e.g. Galápagos fur seals (*A. galapagoensis* (Heller, 1904)), and Galápagos sea lions (*Zalophus wollebaecki* (Sivertsen, 1953))] display the longest lactations (2-3 yr), presumably as a bet-hedging strategy to buffer against large interannual variation in marine productivity. Although this hypothesis has received recent support from analyses controlling for phylogeny and body size (Schulz and Bowen 2005), data from species breeding at temperate latitudes suggest that nearly every other aspect of maternal strategy (e.g. foraging cycle duration and milk characteristics) is more strongly influenced by prey ecology and distribution (Francis et al. 1998).

One of the difficulties of interspecific comparisons is the inability to control for confounding effects of environmental differences. The problem is often unavoidable because breeding distributions of species do not overlap. However, several otariid species with widely differing lactation duration have overlapping distributions [e.g. northern fur seals and California sea lions (*Zalophus californianus* (Lesson, 1828))], and can even be found breeding syntopically at certain sites. In this situation, the environment exhibits the same levels of productivity, seasonality, and predictability, yet maternal expenditure is spread over periods of different duration. Thus, it is not clear what particular strategy a female should adopt, and how her pup should respond because different trade-offs may be under selection (Peaker 1989, Owen-Smith 2004). Some physiological and behavioural traits of the maternal strategy may have become more rigid, especially in species that have evolved under relatively predictable environmental regimes at the core of their distribution, while others may be more flexible (König and Markl 1987, Rehling and Trillmich 2007). Clearly, trade-offs acting on pups are part of the observed strategies.

Two otariid species inhabiting the Southern Ocean are particularly suited for this topic – Antarctic fur seal (AFS) and subantarctic fur seal (SFS) – because they are closely related (Bininda-Emonds et al. 1999), and are morphologically very similar (Payne 1979, Bester and Van Jaarsveld 1994), yet exhibit a large disparity in lactation duration: 116 d in AFS (Costa et al. 1988, Lunn et al. 1993) and 300 d in SFS (Kerley 1987, Guinet and Georges 2000). AFS breed primarily south of the Antarctic Polar Front (APF), while SFS do so around the Subtropical Front (STF) (Bonner and Harrison 1981), so represent the subpolar and temperate maternal strategy in the continuum described above. However, both species breed syntopically at a few locations where habitat differences between species are likely to be minimal, facilitating the interpretation of comparative analyses. Recent comparisons of the foraging ecology of lactating females at Iles Crozet have shown important differences in their diving behaviour (Luque et al. 2007*a*) that appear to be driven by greater physiological constraints in AFS (Luque et al. 2008), despite largely overlapping foraging areas. AFS pups at this location show higher resting and field metabolic rates than SFS pups (Arnould et al. 2003). Furthermore, growth studies suggest that AFS pups trade-off fat storage for increased lean body mass growth, compared to SFS pups (Luque et al. 2007*b*). However, the mechanisms linking maternal strategy and pup development remain unclear.

In this study, I investigated the process linking two major aspects of maternal strategy – attendance and milk delivery – to the associated dynamics of preweaning pup growth in AFS and SFS. Specifically, my aim was to determine whether milk intake, measured as pup mass gain during maternal attendances, and the ensuing mass loss during maternal foraging trips, differed between species to account for the observed overall differences in growth patterns. Given the previously reported interspecific differences in metabolism, I also compared body composition (total body lipid) and milk composition to assess possible differences in energy allocation by pups. Based on previously reported differences in pup metabolism and maternal foraging behaviour, I hypothesize that lactating AFS females show greater rate of maternal expenditure during lactation than SFS, and that AFS pups should show greater mass gain during maternal attendances.

5.2 Methods

5.2.1 Study site and animals

Research was carried out at La Mare aux Elephants (46°22'29" S, 51°40'13" E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001-02 (4 December - 25 March) and 2002-03 (1 December - 16 March) breeding seasons (2001 and 2002 hereafter). The site consists of two adjacent AFS and SFS colonies, where peak pupping dates were found to be 5 and 15 December (2001: 164, and 2002: 167 pups) for AFS, and 25 and 30 December (2001: 80, and 2002: 91 pups) for SFS. During both pupping periods, 277 fur seal pups were individually marked with a numbered piece of tape temporarily glued to the fur on top of the head. At approximately 30 d of age, pups were permanently marked by attaching a tag to the trailing-edge of both fore-flippers. Because absolute age was not known for all pups, relative age was defined as the number of days elapsed since individuals were first seen, which was taken as day zero. The difference in peak pupping dates between species was taken into account by adding the corresponding value from each breeding season (2001: 20, and 2002: 15 d) to the relative age of AFS pups. Molting began in February for both species, so 1 February was used to differentiate pre- and postmolting pups.

As part of concurrent growth studies (Luque et al. 2007*b*), pups were weighed to the nearest 0.05 kg at first capture, and every 5-9 d thereafter, on a 25-kg capacity digital suspension balance (Salter Brecknell, ElectroSamson). Straight-line body length (to the nearest 0.5 cm) was also measured upon first capture, and every 12-16 d thereafter. Mothers of a subset of marked pups (AFS: $n = 49$; SFS: $n = 47$) were equipped with time-depth recorders (TDRs) and Platform Transmitter Terminals (PTTs) throughout both study periods as part of research on maternal foraging behaviour (Luque et al. 2007*a*). Body mass (to the nearest kg) and body length (to the nearest cm) of instrumented females were recorded immediately before and after deployment, and again when females were recaptured and tagged to recover instruments after 1-11 foraging trips (Jiang et al. 2002). Maternal attendance was determined from the times of arrival and departure to and from the colonies recorded by the instruments. Maternal attendance was also monitored by visually searching the colonies three times per day (09:00, 14:00, and 18:00), and recording the presence of mothers of marked pups.

5.2.2 Body composition

Pups were selected pseudo-randomly for body composition analysis throughout both study periods. The selection of study of pups was ultimately constrained by the availability of marked pups known to have been fasting for a minimum of 24 h, to allow for digestion of milk consumed during the last maternal attendance. Body composition was measured using hydrogen isotope dilution techniques (Costa et al. 1987). Pups were weighed and measured before collecting a background blood sample

(5 ml) from an inter-digital vein in a hind-flipper. They were subsequently given an intramuscular injection of a weighed dose of tritiated water (HTO; approximately 1 ml, 7.4 mBq $\cdot$ ml^{-1} or 50 μCi $\cdot$ ml^{-1}). Pups were kept in an enclosure for 3 h to allow equilibration of injected tritiated water with body water, and a second blood sample (5 ml) was collected to determine total body water (TBW).

Blood samples were kept at about 4°C for several hours before being centrifuged at 3000 rpm for 10 min, and the plasma fraction separated. Aliquot samples (1-2 ml) were stored frozen (-20°C) until laboratory analysis were performed in May 2002 and 2003. Thawed subsample aliquots of plasma (0.1-0.2 ml) were distilled into pre-weighed scintillation vials (Ortiz et al. 1978). Vials were re-weighed to obtain the mass of distilled water (±0.1 mg), and a scintillant (5 ml Pico Fluor; Canberra Packard) was added to each vial. The specific activity of tritium was counted for 10 min using a Packard Liquid Scintillation Counter (1600TR), with correction for quenching by means of the sample channels ratio and an external standard to set the counting window for the vials. Samples were analyzed in duplicate and each vial was counted twice. Subsamples of the injectant (0.2 ml) were also counted similarly and at the same time as the vials with plasma samples to determine the specific activity of the tritium injected.

Total body water was calculated from HTO dilution space using equation 5 from Bowen et al. (1998) ($TBW = 0.003 + 0.968 \cdot H - space$). Lean body mass was calculated from TBW, assuming a hydration constant of 74.7% (Arnould et al. 1996*b*), and total body lipid (TBL) was calculated by subtracting lean body mass from total body mass.

5.2.3 Milk composition

Upon recapture, lactating females equipped with TDRs were given an intramuscular injection of oxytocin (1 ml, 10 UI ml^{-1}), and a milk sample (5-30 ml) was collected by manual expression and stored in a plastic vial at -20°C until laboratory analysis were performed (May-June 2002 and 2003). Samples from mothers of two AFS and four SFS pups that were not instrumented were also collected. Frozen milk samples were thawed at room temperature (20°C) and thoroughly mixed using a high-speed stirring rod. Water content was determined by drying subsamples (1.5-2.0 g) in preweighed aluminium foil trays for 72 h at 80°C in an oven. The dried samples were cooled in a dissicator before weighing them again to determine water content by subtraction.

Protein and lipid content were determined using the relationships between elemental carbon (C), hydrogen (H), and nitrogen (N), studied in AFS from South Georgia (Gnaiger and Bitterlich 1984, Arnould et al. 1995). Subsamples of the dried solids (200-250 mg) from water content analyses were placed in preweighed tinfoil containers, and stored in a dissicator until they were analyzed in an automatic CHN analyser (Perkin Elmer, Elemental Analyser 2400 CHN), by using a certified reference standard (supplied by Laboratory Services Division, University of Guelph, Ontario). Protein and lipid content were calculated using the measured C, H, and N proportions of dry mass following procedures outlined in Gnaiger and Bitterlich (1984), modified to account for the particular characteristics of fur seal milk (Arnould et al. 1995).

Gross energy content was calculated by multiplying the derived lipid and protein compositions by standard values of energy density of these components (lipid: 38.12 kJ · g^{-1}; protein: 23.64 kJ · g^{-1}) (Perrin 1958). Carbohydrates typically represent less than 0.5% of total milk volume, equivalent to less than 0.2% of gross energy in pinniped milks (Oftedal et al. 1987), so were not considered in the calculation of gross energy content.

Due to problems with the CHN analyser, protein, lipid, and associated gross energy content could not determined for 12 AFS and 13 SFS samples. Therefore, the strong negative relationship between lipid and water content (Arnould et al. 1995, Goldsworthy and Crowley 1999) was used to recalculate the lipid and gross energy content of all samples to allow for comparisons. From CHN analyses, lipid (%) could be reasonably ($r^2 = 0.79$, residual SE=0.04, $P < 0.001$) predicted from water content (%):

$$lipid = 78.44 - 82.14 \times water \tag{5.1}$$

Consequently, gross energy content was strongly related to water content ($r^2 = 0.97$, residual SE=0.55, $P < 0.001$):

$$energy = 33.44 - 0.34 \times water \tag{5.2}$$

which is nearly identical to the relationship observed in these two species at Macquarie Island (Goldsworthy and Crowley 1999), and in AFS at South Georgia (Arnould and Boyd 1995*a*). Lipid and gross energy content were recalculated for all samples using these equations for comparisons.

5.2.4 Pup mass changes

Body mass changes due to maternal attendance patterns were studied by observing the attendance of mothers of marked pups, and weighing pups daily when mothers were at sea. The colonies were monitored throughout the day and study period, so care was taken to weigh pups soon after departure of the mother, and daily until her return.

Using t_0 to denote the time when a pup was weighed following its mother's departure to sea, and t_1 the time when it was weighed immediately before her return, respectively, mass-specific rate of mass loss (MSRML, $\% \cdot d^{-1}$) was defined as:

$$MSRML = \frac{log\ m_1 - log\ m_0}{\Delta t} \times 100 \tag{5.3}$$

where m_0 and m_1 represent the mass of the pup at t_0 and t_1, respectively, and $\Delta t = t_1 - t_0$ (d).

Lactating females perform overnight foraging trips (OFTs) at La Mare aux Elephants (Luque et al. 2007*a*), which are not reliably detected by observers in the field. Therefore, mass gained by pups during maternal attendances was calculated only for pups whose mothers were instrumented. Using subscript 2 to indicate the time when a pup was weighed following its mother's departure (after t_1) the absolute mass gained by pups during maternal attendances was defined as $m_2 - m_1$. Only pup mass records obtained no more than 1 d before the beginning or 1 d after the end of a maternal attendance were considered for calculation of absolute pup mass gain.

5.2.5 Statistical analyses

A small proportion of marked pups (5-10%) were selected for body composition or mass changes analyses more than once throughout the study period, so a single record was chosen at random to avoid pseudoreplication and give all pups the same weight during analyses. Factors influencing variation in TBL, milk components, and mass changes were examined using linear multivariate analyses of covariance (Tabachnick and Fidell 2001). Model selection began by including all main effects and interaction terms, and subsequently removing in a stepwise manner terms that did not contribute significantly to the design, while keeping the model as simple as possible. The Akaike Information Criterion (AIC) was used to guide the decision process (Venables and Ripley 2002). All data analyses were performed with the `GNU R` system (R development Core Team 2007).

5.3 Results

5.3.1 Body composition

Variation in total body lipid (TBL) stores of SFS and AFS pups was most parsimoniously accounted for by body mass, species, and sex (Table 5.1). The selected model did not include interactions between any of these factors, showing that SFS ($F_{1,94} = 4.57$, $P = 0.03$) had significantly higher TBL stores for any given body mass than AFS (Figure 5.1a). Female pups had higher TBL ($F_{1,94} = 5.63$, $P = 0.02$) than male pups of the same body mass. SFS and female pups had, on average, 1.5% and 1.2% higher TBL stores (percent body mass) than AFS and male pups, respectively (Table 5.2).

Post-molt pups had significantly higher TBL (percent of body mass, Figure 5.1b) than pre-molt pups in both species ($F_{1,95} = 14.81$, $P < 0.001$), without intersexual differences nor interactions between species and sexes affecting the comparison (ANOVA test significance of inclusion/removal of model terms $P > 0.1$, all cases). Although SFS pups had higher TBL than AFS throughout the study period, the difference was not significant ($F_{1,95} = 3.58$, $P = 0.06$). The same result was found if relative age, rather than molting stage, was used as covariate.

5.3.2 Milk composition

AFS and SFS milk was composed of about 40% water in both species (Table 5.3). Protein content, determined from CHN analysis of subsamples from 81 adult females, was approximately 10% (Table 5.3). Water content decreased significantly with pup relative age ($F_{1,99} = 51.76$, $P < 0.001$), and the pattern was similar for both species ($species \times relative\ age$ interaction: $F_{1,99} = 0.48$, $P > 0.1$). Consequently, predicted lipid and gross energy content increased during lactation (Figure 5.2a). At any given age, pups of both species consumed milk with similar lipid content, although the value was marginally higher for SFS pups ($F_{1,99} = 3.13$, $P = 0.08$). Lipid content increased by approximately 10% between pre-molt and post-molt stages of lactation (Figure 5.2b), again without interaction with species ($F_{1,99} = 0.76$, $P > 0.1$), and marginally higher values for SFS pups ($F_{1,99} = 3.53$, $P = 0.06$). Gross energy content also followed this pattern of variation with pup relative age. Therefore, data were pooled, and gross energy content of milk ($\mathrm{kJ} \cdot \mathrm{g}^{-1}$) could be predicted from pup relative age (d) using ($r^2 = 0.33$, residual $SE = 2.44$, $P < 0.001$):

$$gross\ energy = 17.21 + 0.072 \times age \tag{5.4}$$

5.3.3 Pup mass changes during maternal foraging cycles

Mass gained by pups during maternal attendances was not significantly related to sex, nor to body mass immediately prior to arrival of their mothers (Table 5.4). Mass gain averaged 0.85 kg during each maternal attendance, but AFS gained significantly more mass ($F_{1,58} = 6.28$, $P = 0.02$) than SFS (Table 5.5), at about 41 d relative age. Mass gain was similar for both sexes ($F_{1,58} = 0.1$, $P > 0.1$), and pup sex did not influence interspecific comparisons ($F_{1,58} = 0.6$, $P > 0.1$).

Variation in mass gain was parsimoniously accounted for by the duration of preceding maternal foraging trip (FTD), species, and the interaction between these factors (Table 5.4). Thus, the overall interspecific differences in mass gain reflected the more rapid increase in mass gain per unit increase in maternal foraging trip duration in AFS (Figure 5.3). The relationship did not hold for OFTs, when mass gain could be as high as 1.12 kg, particularly among AFS (Figure 5.3). Small sample size prevented inclusion of foraging trip type in the model selection procedure, so data from OFTs were excluded from comparisons.

Absolute energy gain was calculated for all pups using equation (5.4) to predict energy content from relative age, and multiplying the result by mass gain. Energy gain increased with relative age at a similar rate for both species (Figure 5.4), but AFS gained more energy at any given age than SFS ($F_{1,53} = 5.13$, $P = 0.03$).

Study of mass-specific rate of mass loss (MSRML) during maternal foraging trips required inclusion of a $species \times sex$ ($F_{1,83} = 7.1$, $P < 0.01$) interaction term. Interspecific differences were found only among female pups, where AFS had higher MSRML than SFS ($F_{1,37} = 10.7$, $P = 0.002$) (Table 5.5). Furthermore, female AFS pups had significantly higher MSRML than males ($F_{1,49} = 13.4$, $P < 0.001$), whereas there was no significant difference in SFS pups ($F_{1,33} = 0.12$, $P > 0.1$).

5.4 Discussion

I show that, under conditions of syntopy, AFS pups: i) consume greater quantities of milk, with the difference being larger during maternal attendances preceded by long foraging trips (LFTs) lasting more than about 3 d, ii) have higher energy intake at any given age, and iii) have significantly smaller TBL stores than SFS pups of the same mass. These differences support the hypothesis stating that rate of energy expenditure is greater in lactating AFS females, and provide further evidence that physiological constraints on maternal strategy may be stronger in this species.

I made two crucial assumptions interpreting these results. First, that observed absolute mass gain is equivalent to milk intake. Other methods exist to measure milk intake in the field, such as isotopic analyses to estimate water intake (Costa et al. 1987). These methods do not necessarily provide more accurate estimates of milk intake because they tend to overestimate metabolic water production when water intake from sources other than milk is substantial, which leads to underestimation of total water intake attributed to milk (Lea et al. 2002*a*). Arnould et al. (1996*a*) showed good agreement between actual and estimated water intake in AFS pups from South Georgia. Anecdotal evidence from this study suggests that freshwater drinking does occur at Ile de la Possession on particularly warm days ($> 12°$C), but the extent to which it occurs is unknown. The absolute mass gain values found here are similar to those found at Iles Kerguelen (Guinet et al. 2000) and Macquarie Island (Guinet et al. 1999) for AFS, and at Amsterdam Island for SFS (Georges and Guinet 2000*b*). By setting strict rules on the selection of pup mass records, and using the most accurate information on maternal attendance, comparisons of milk intake using this method seem to be valid, and may be more accurate than using more expensive and time-consuming methods.

Second, I assumed that the relationship between milk lipid content and age (Figure 5.2) described the relationship for all study pups. Milk composition was not determined for all pups in the absolute mass gain study, so it is possible that the milk they consumed had a different lipid content than that predicted for their age, and thus carried a bias to the calculation of energy intake [equation (5.4)]. Milk composition is known to vary with mammary evacuation in several terrestrial mammals (Oftedal 1984), but this effect has not been found in AFS (Arnould and Boyd 1995*a*). All samples in this study were collected soon after females returned from their foraging trips, so any potential effect of this source of variation was probably small. Nonetheless, milk samples collected serially from individuals would allow a more rigorous analysis accounting for interindividual differences. In combination with larger samples, this would also help clarify the biological significance of the slightly larger lipid content in SFS, adjusted for pup age, which in turn influence energy intake calculations.

Removing the effect of pup age, I did not find significant differences in milk lipid, and hence, gross energy content between species. The average lipid content of AFS milk in this study appears to be slightly larger than that reported for Macquarie Island (in syntopy with SFS, Goldsworthy and Crowley 1999) and South Georgia (Arnould and Boyd 1995*a*), covering similar stages of lactation. The values for SFS milk also appear slightly larger in this study than those reported for Macquarie Island Goldsworthy and Crowley (1999), and similar to those obtained at Amsterdam Island (Georges et al. 2001), for the same period of lactation and maternal attendance characteristics. In both species, however, milk lipid content changed similarly with pup age in all studies. These comparisons are in agreement with Francis et al.'s (1998) hypothesis stating that milk characteristics reflect local foraging habitat more than latitudinal variation in marine productivity, seasonality, and predictability.

Absolute pup mass gain during maternal attendances increased with the duration of the preceding foraging trip of mothers, as has been found previously for both species (Guinet et al. 1999, Guinet and Georges 2000, Guinet et al. 2000). However, this increase was more pronounced in AFS, which was reflected in the larger average mass gained by AFS pups. Interestingly, lactating females of both species returning from OFTs provided pups with a wide range of milk quantities that did not follow the same relationship observed during LFTs. In both species, there is no obvious pattern in the occurrence of OFTs (Luque et al. 2007*a*), so the large variation in pup mass gain after these trips may during lactation are Absolute mass gain did not differ between sexes in both species, in agreement with substantial evidence for equality in maternal expenditure between sexes (Ono and Boness 1996, Lunn and Arnould 1997, Guinet et al. 1999, Guinet and Georges 2000, Guinet et al. 2000).

Supporting my hypothesis, AFS pups had significantly larger average pup mass (milk) gain, and they also gained more mass per day their mothers spent at sea, particularly during the longest LFTs. Total energy gain was also larger in AFS pups at any given age, confirming that the differences in mass gain were not due to uneven sampling of LFTs between species. This is consistent with evidence of larger foraging effort and access to prey patches of better quality in lactating AFS females (Luque et al. 2008). It also suggests that the rate of energy transfer from mother to pup during lactation is higher in AFS, which may reflect adaptations of each species' maternal strategy to the typical marine habitat at the core of their geographical distributions, and are more rigid aspects of the maternal strategy. Milk composition and consumption data from other otariids breeding at temperate latitudes is still scarce. However, similar low values were found in Australian fur seals (*Arctocephalus pusillus doriferus* (Wood Jones, 1925)) in southern Australia (Arnould and Hindell 2001, 2002), and SFS in Amsterdam Island (Georges and Guinet 2000*b*, Guinet and Georges 2000) (10 mo lactation, both species), compared to subpolar AFS and northern fur seals (Donohue et al. 2002), has been attributed to lower marine productivity at those sites. Thus, my study of this aspect of maternal strategy is congruent with the productivity-seasonality hypothesis (Gentry et al. 1986), and supports a recent analysis (Schulz and Bowen 2005).

I found also that MSRML was higher in AFS pups, but the difference existed only among females. Furthermore, females had higher MSRML than males only among AFS pups, suggesting that previously reported differences in fasting metabolism between sexes (Arnould et al. 1996*a*) may be species-specific. Indeed, MSRML did not differ between sexes in SFS at Amsterdam Island (Beauplet et al. 2003). Similar to the results shown here, MSRML was higher for females than males among AFS at Iles Kerguelen (Guinet et al. 2000). In both species, female pups seem to rely more heavily on protein catabolism when fasting than male pups, despite having relatively larger fat stores (Arnould et al. 1996*a*, Beauplet et al. 2003). If this intersexual difference is present in both species, why is MSRML higher in females only in AFS pups? Mass-specific resting and field metabolic rates are higher in female AFS pups, compared to conspecific male pups (Arnould et al. 2001). Field metabolic rate did not differ significantly between sexes in SFS (Beauplet et al. 2003), but studies comparing resting metabolic rate between sexes in this species await more detailed analyses (Arnould et al. 2003). The answer to this question may lie in physiological adaptations to the extremely long, by otariid standards, fasting durations experienced by SFS pups (Georges and Guinet 2000*b*, Beauplet et al. 2003), forcing females to adopt a strategy similar to that of males.

This study did not cover the entire lactation period of SFS, but data from two lactating females that were monitored during July and August 2003, showed foraging trips lasting more than a month in both cases (Luque et al. 2007*a*), which does not differ from findings at Amsterdam Island (Georges et al. 2000*b*, Beauplet et al. 2004). Therefore, SFS pups at Ile de la Possession may experience similar increases in fasting duration throughout lactation as those observed at lower latitudes. The presence of two different patterns of MSRML between syntopic populations of these species suggests that they are more rigid aspects of pup growth strategy. The differences in body composition reported here confirm those presented previously with a smaller sample size during February 2002 (Arnould et al. 2003), and are consistent with differences in pattern of physical growth over the initial 100 d of lactation (Luque et al. 2007*b*). Our analyses suggest that, compared to SFS, AFS pups adopt a growth strategy that requires higher levels of maternal energy expenditure that is used for proportionally larger development of lean body mass, in preparation for weaning at a younger age.

Some aspects of maternal and pup growth strategies (maternal expenditure and pup fasting metabolism) in otariids may have evolved in response to weaning at different times of marine productivity cycles. Whereas AFS pups wean at the time of lowest productivity, SFS pups do so during the following peak in productivity. Therefore, there may be stronger selection for lean body mass growth in AFS during their briefer lactation to allow for adequate physical and physiological maturation needed for successful foraging at a time of reduced prey availability. Conversely, there may be stronger selection for development of larger fat stores in SFS pups during summer, in preparation for prolonged periods of fasting in winter. Lean body mass (muscle) growth may become more important for SFS during winter, as weaning approaches during a period of increasing prey availability. Although this seems intuitive, comparative studies of species with differing lactation durations at syntopic sites facilitate interpretation and highlight the importance of constraints acting on mothers vs. those acting on offspring.

Table 5.1. Changes in Akaike Information Criterion (AIC) and deviance during stepwise procedure for selecting model of variation in pup total body lipid stores. The procedure began with a model including body mass, species, sex, and all their interactions. Terms shown produced significant reductions in AIC, so were not retained. Final model included additive effects of body mass, species, and sex

Effect tested	Deviance	Residual *df*	Residual deviance	AIC
Full model		90	18.3	-148.5
body mass × *species* × *sex*	0.32	91	18.6	-148.7
body mass × *species*	< 0.001	92	18.6	-150.7
species × *sex*	0.19	93	18.8	-151.7
body mass × *sex*	0.20	94	19.0	-152.7

Table 5.2. Total body lipid stores (relative to body mass) were higher in subantarctic (*Arctocephalus tropicalis* (Gray, 1872); SFS) than in Antarctic (*A. gazella* (Peters, 1875); AFS) fur seal pups

Species	Sex	N	Relative age (d)	Body mass (kg)	Total body lipid (%)
AFS	Females	23	35.3 ± 7.86	8.5 ± 0.34	26.3 ± 0.01
	Males	24	40.3 ± 7.65	9.6 ± 0.49	25.9 ± 0.01
	Both	47	37.8 ± 5.39	9.0 ± 0.31	26.1 ± 0.008[a]
SFS	Females	28	48.2 ± 4.77	7.3 ± 0.32	28.5 ± 0.01
	Males	23	42.1 ± 5.72	8.7 ± 0.44	26.5 ± 0.01
	Both	51	45.4 ± 3.67	8.0 ± 0.28	27.6 ± 0.008[a]

[a] Significant interspecific differences ($F_{1,94} = 4.57$, $P = 0.03$), accounting for differences between sexes ($F_{1,94} = 5.63$, $P = 0.02$)

Table 5.3. Composition of milk from Antarctic (AFS) and subantarctic (SFS) fur seal females, at 36.9 d (range: 9–87) and 37.3 d (range: 0–82) of lactation, respectively

Component	AFS ($N = 51$)	SFS ($N = 51$)	*F-ratio*	P
Water (%)	41.2 ± 1.20	38.6 ± 1.26	2.22	0.14
Lipid (%)[a]	44.6 ± 0.97	46.7 ± 1.03	—	—
Protein (%)[b]	9.8 ± 0.59	9.7 ± 0.61	0.01	0.93
Gross energy ($\mathrm{kJ} \cdot \mathrm{g}^{-1}$)[c]	19.5 ± 0.40	20.3 ± 0.43	—	—

[a] Determined from relationship between water and lipid content of subsamples (AFS: 39, SFS: 38) using an empirical stoichiometric relationship between elemental carbon (C), hydrogen (H), and nitrogen (N) (Arnould et al. 1995). ANOVA not shown; same as for water

[b] Obtained from empirical stoichiometric relationships between C, H, and N in subsamples (*a*)

[c] Calculated from equation equation (5.2), so ANOVA not shown; same as for water

Table 5.4. Changes in Akaike Information Criterion (AIC) and deviance during stepwise procedure for selecting model of variation in mass gained during maternal attendances. The procedure began with a model including the duration of the preceding maternal foraging trip (FTD), species, sex, initial mass (m_1), and all their interactions. Terms shown produced significant reductions in AIC, so were not retained. Final model included additive effects of FTD, species, and interaction between species and FTD

Effect tested	Deviance	Residual *df*	Residual deviance	AIC
Full model		34	4.41	-79.92
$FTD \times species \times sex$	0.024	35	4.43	-81.69
$FTD \times sex$	0.025	36	4.46	-83.45
m_1	0.173	37	4.63	-83.81
$species \times sex$	0.186	38	4.82	-84.11
sex	< 0.01	39	4.82	-86.10

Table 5.5. Mass gained during maternal attendances, and mass-specific rate of mass loss (MSRML) during maternal foraging trips, by Antarctic (AFS) and subntarctic (SFS) fur seal pups

Species	Sex	Absolute mass gain (kg)			MSRML (%)		
		N	Rel. age (d)	Mean±SE	N	Rel. age (d)	Mean±SE
AFS	Females	14	37.9 ± 6.31	0.99 ± 0.118	23	33.6 ± 4.41	3.56 ± 0.190^{b}
	Males	20	45.0 ± 5.45	0.95 ± 0.103	28	38.5 ± 4.48	2.60 ± 0.179
	Both	34	42.1 ± 4.11	0.96 ± 0.076^{a}	51	36.3 ± 3.15	3.04 ± 0.146
SFS	Females	18	42.7 ± 4.70	0.61 ± 0.107	16	51.6 ± 9.62	2.61 ± 0.219^{b}
	Males	8	36.9 ± 7.80	0.77 ± 0.209	19	35.1 ± 4.80	2.71 ± 0.193
	Both	26	40.9 ± 3.99	0.66 ± 0.097^{a}	35	42.6 ± 5.22	2.67 ± 0.143

[a,b] Significant interspecific differences: $F_{1,58} = 6.28$, ($P = 0.02$) and $F_{1,37} = 10.7$ ($P = 0.002$), respectively

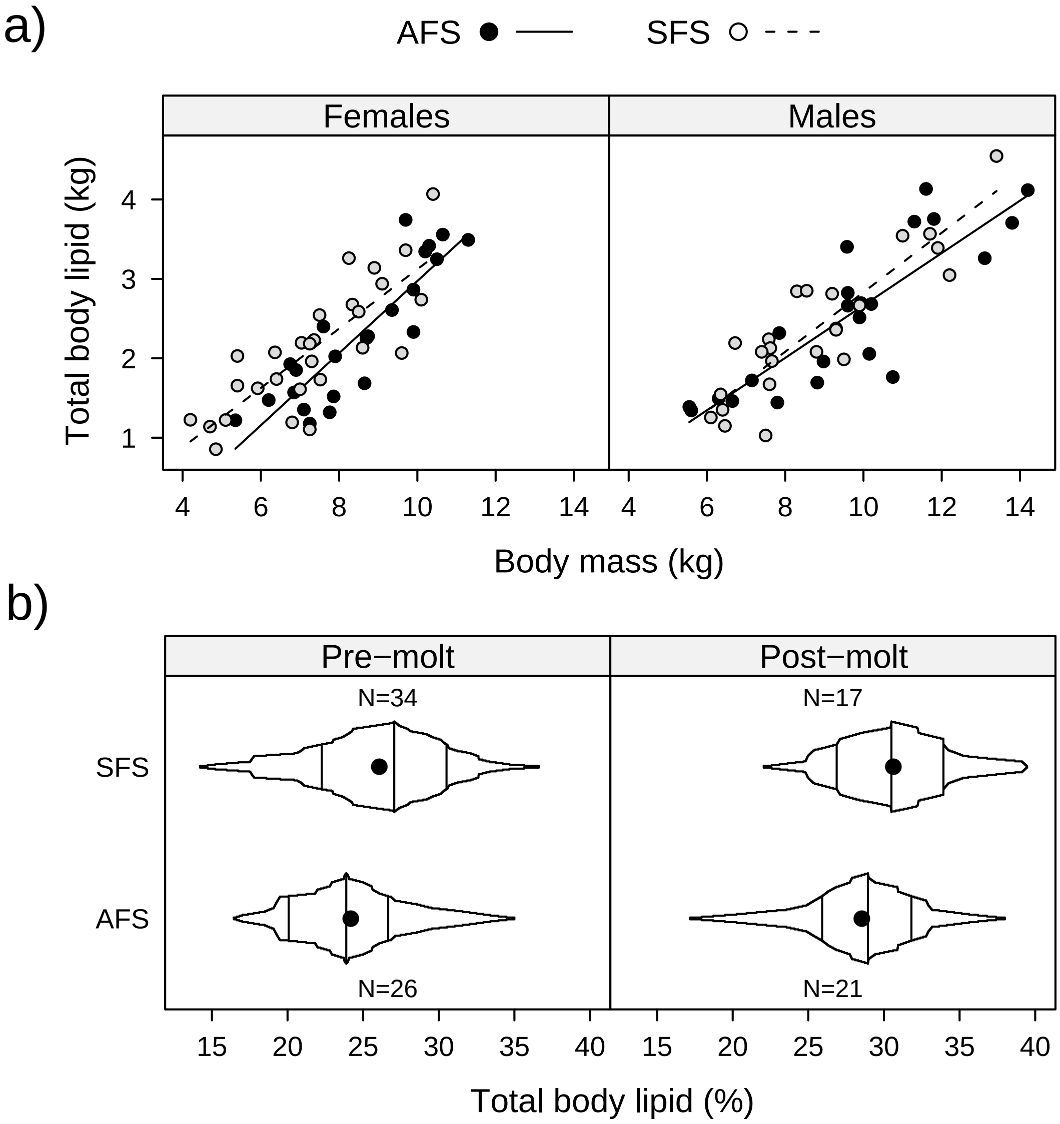

Figure 5.1. a) Female pups had higher total body lipid (TBL) stores, relative to body mass, than male pups in Antarctic (AFS) and subantarctic (SFS) fur seals. Accounting for differences between sexes, SFS pups had higher TBL stores than AFS (summary in Table 5.2). b) Post-molt pups had significantly higher TBL (as percent of body mass), compared to pre-molt animals, but interspecific differences were not significant. Shape of the box-percentile represents all quantiles from first through 99th, the mean (circle), median, and 25th and 75th quantiles (solid vertical reference lines) of the distributions

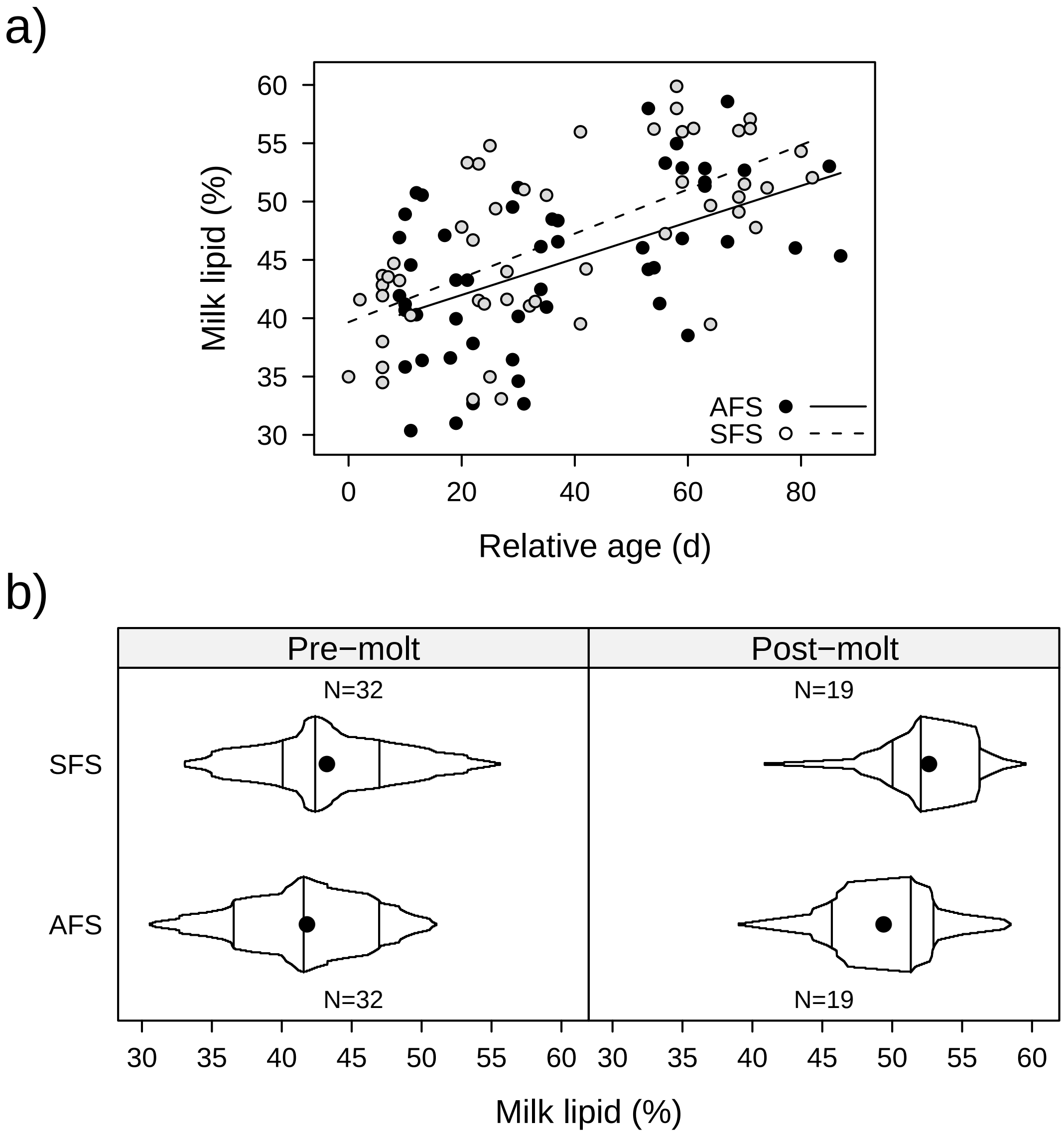

Figure 5.2. a) Lipid content (%) of milk increased with relative pup age in AFS and SFS females, without significant differences between species (summary of milk composition in Table 5.3). b) Milk secreted during the post-molt period had significantly higher lipid content than during the pre-molt period for both species. Shape of the box-percentile represents all quantiles from first through 99th, the mean (circle), median, and 25th and 75th quantiles (solid vertical reference lines) of the distributions

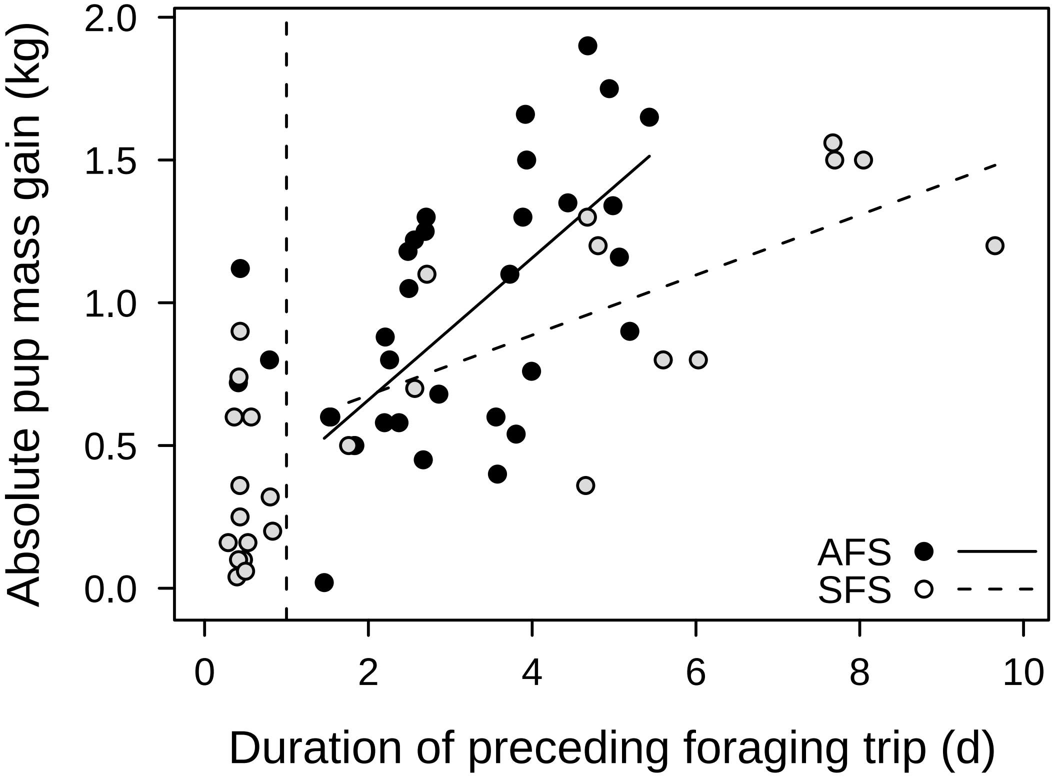

Figure 5.3. The absolute mass gained (milk) by AFS and SFS pups during a maternal attendance period increased with the duration of their mothers' preceding foraging trip. The relationship was stronger during long foraging trips (LFTs) than during overnight foraging trips (OFTs), and AFS pups gained more mass per unit increase in maternal foraging trip duration than their congeners. The vertical dashed line separates OFTs from LFTs

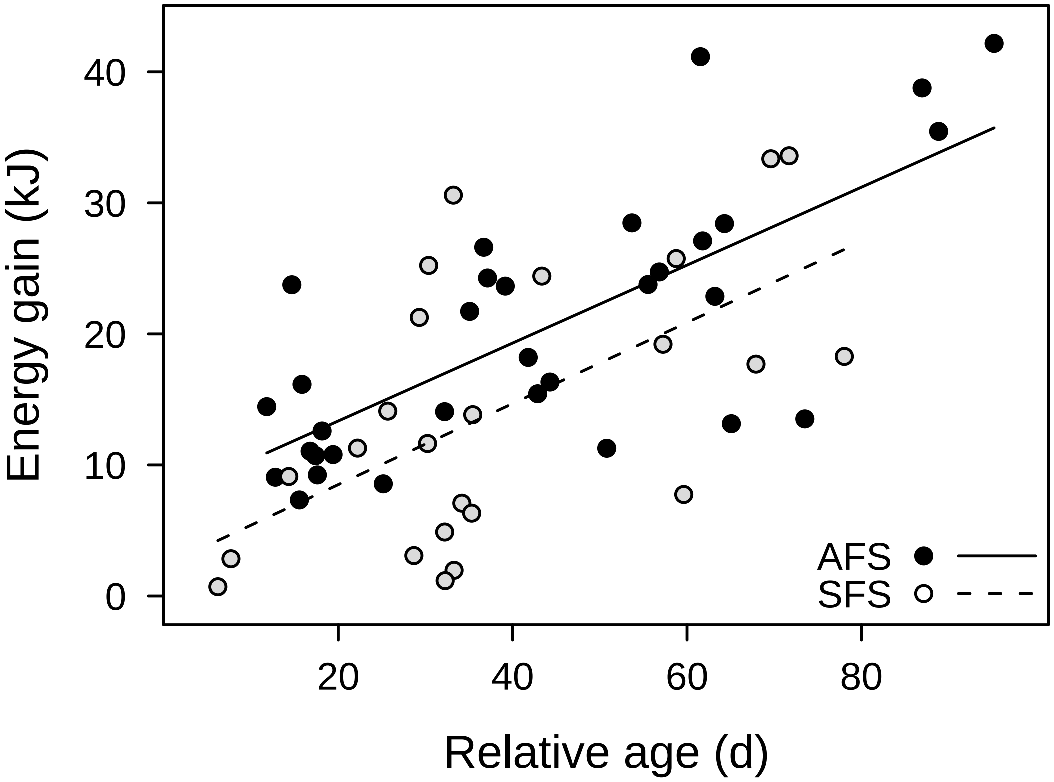

Figure 5.4. The absolute energy (from milk) gained by AFS and SFS pups during a maternal attendance period increased with relative age. At any given age, AFS pups gained more energy than their congeners. Energy gain was calculated from relationship between milk gross energy content and relative age for both species combined

Part III

Synthesis

I compared several aspects of maternal and pup growth strategies in two closely related, and morphologically similar, otariid species differing primarily in lactation duration and global distribution. My main motivation was to address prevailing weaknesses in interspecific comparisons attempting to explain variation in lactation duration among otariids, namely the inability to control for confounding effects of differences in environment. Therefore, I took advantage of a rare situation where species with widely differing lactation duration and global distribution breed sympatrically. Local foraging habitat was recognized as a major determinant of foraging behaviour of females during lactation (Francis et al. 1998), but are females constrained by different lactation duration? Offspring influence the physiology and behaviour of their mothers and viceversa, so these interactions are obviously an important part of the environment in which lactation occurs, and cannot easily be disentangled from other influences. At the expense of reducing the number of species in comparisons, I used a system where differences in physical environment are removed, to provide insights into mechanisms driving variation in maternal strategies in otariids.

In Part I of my thesis, I compared the major aspects of foraging ecology between lactating Antarctic, AFS and subantarctic fur seal, SFS females. I showed that:

1. Lactating females of both species fed on the same myctophid fish prey over largely overlapping areas, with minor but important differences in the proportion of species consumed.

2. In common with other sites where both species breed sympatrically, and in contrast with allopatric sites, lactating females displayed a bimodal distribution in foraging trip duration, with females spending greater foraging effort in overnight foraging trips (OFTs).

3. SFS females made longer long foraging trips (LFTs), more frequent OFTs, and

spent a smaller proportion of their foraging cycle (attendance and foraging trip) at sea. Furthermore, they showed less diel variation in diving behaviour and effort, suggesting that they followed the nycthymeral migrations of their prey to a smaller extent than AFS. Diving occurred almost exclusively at night in both species, but SFS females dove deeper and for longer periods.

4. Species differed in physiological constraints when foraging during lactation, as inferred from the greater behavioural aerobic dive limit (ADL) in SFS, which may explain the longer and deeper diving observed in this species. However, AFS females had higher propensity to dive anaerobically.

5. Structure of prey patches, as revealed by temporal structure of diving bouts, suggests that AFS females exploited more patches per unit time, and remained in them for briefer periods of time. Considering the differences in behavioural ADL in an index of patch quality (IPQ), AFS females appeared to forage in patches of better quality, at the cost of greater foraging effort[1].

In Part II, I considered aspects of the maternal strategy related to the delivery of energy (via milk) to offspring, and the allocation of that energy into growth. To summarize these findings:

1. Body shape differed significantly between species from birth. Growth during the first 100 d of lactation involved the acquisition of a longer, more slender body with larger foreflippers in AFS.

2. Allometric analysis showed that body shape differences present at birth were exacerbated during growth. AFS pups seemed to reach adult body shape faster than SFS pups, suggesting that they are physically more mature at 100 d.

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[1] Section 3.1 was a necessary technical development to allow the comparisons in the following section (summarized here) to be done more rigourously than was possible with previously available methods.

3. AFS pups consumed greater quantities of milk, both on absolute terms, and adjusted for differences due to maternal foraging trip duration. Furthermore, milk composition did not differ between species, so that total energy intake was significantly higher in AFS at any given age.

4. SFS pups had proportionally larger total body lipid reserves, and had lower resting and daily metabolic rates than AFS pups. Oxygen storage capacity also appeared to be smaller in SFS pups of the same age.

Globally, these results show evidence of flexibility in aspects of maternal and pup growth strategies in response to similar foraging habitat, and of rigidity in other aspects that might reflect each species' evolutionary history under different regimes of environmental variation. Across most otariids, lactation duration is significantly related to latitude (Schulz and Bowen 2005), supporting an early hypothesis stating that maternal strategies follow regimes of marine productivity, seasonality, and predictability (Gentry et al. 1986). The analyses I presented elaborate on Francis et al.'s 1998 suggestion that local habitat is a major influence on particular characteristics of maternal foraging behaviour, adding that pup growth strategies may be more inflexible than those of their mothers, further constraining how lactating females forage. Pups' growth may be attuned to weaning at different ages without first-hand knowledge of the environment, which their mothers possess, so their physiology is likely to be a stronger influence on their mothers' behaviour than viceversa.

A major feature of foraging behaviour in both species at Ile de la Possession is the presence of two types of foraging trip. This was previously reported only at Macquarie Island (Goldsworthy 1999), although it may also occur at Marion Island with more extensive sampling (M. Bester, pers. comm.). It has not been reported at allopatric sites of either species (e.g. Amsterdam Island for SFS, or South Georgia for AFS). Duration of LFTs were at the lower end of values reported for both species. Thus, these aspects of maternal strategy display great plasticity, and appear to be a response to local foraging conditions around the islands. Recent studies (Venables et al. 2007, and references therein) have highlighted the significance of a regular, annual, phytoplankton bloom occurring just north of Ile de la Possession (Figure 1.5), where both fur seal species concentrated their foraging activity (Figure 3, Bailleul et al. 2005). This bloom may be a predictable source of food for plankton and myctophid fish, providing in turn prey availability for fur seals close to the colony.

These observations showed the importance of considering variation in diving behaviour at fine scales throughout foraging trips because they revealed important ecological differences between species that were not apparent at the scale of entire foraging trips. Previous comparisons between sympatric populations of these species at Macquarie and Marion Islands have not shown any major differences at the scale of foraging trips (Bester and Bartlett 1990, Robinson et al. 2002, Kirkman et al. 2003, Bailleul et al. 2005). If actual (rather than behavioural) ADL is greater in SFS across populations, we might expect to find similar differences between species at those sites, using finer scales of analysis. ADL is a fundamental physiological constraint in diving vertebrates (Kooyman 1989), and affects their decisions, even in the same foraging habitat (Mori and Boyd 2004*b*). Therefore, accurate measurements of actual ADL in both species are required to elucidate the physiological basis of the behavioural differences observed in this study. Regardless of the precise mechanism, this difference had important repercussions for the foraging behaviour of fur seals, so is a more rigid aspect of maternal strategy.

These results show evidence that the pattern of physical growth and maturation is faster in AFS, and that it involves fast development of lean body mass (muscle). AFS pups adopted a growth strategy that requires larger maternal expenditure and effort (Chapter 3), regardless of similarities in local foraging conditions experienced by their mothers. These differences may reflect weaning at different times of marine productivity cycles. Whereas AFS pups wean at the time of lowest productivity, SFS pups do so during the following peak in productivity. Therefore, there may be stronger selection for lean body mass growth in AFS during their briefer lactation to allow for adequate physical and physiological maturation needed for successful foraging at a time of reduced prey availability (Burns et al. 2004). Conversely, there may be stronger selection for development of larger fat stores in SFS pups during summer, in preparation for prolonged periods of fasting in winter. Whether lean body mass (muscle) growth is as important for SFS close to weaning as it was for AFS during summer is more difficult to predict. Weaning in SFS occurs in fall during a period of increasing prey availability, so the trade-off between lean body mass vs. fat stores may differ between species. Research on the development of foraging skills by pups of both species, and of the weaning process, is required to clarify what these trade-offs are.

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Appendices

A Software

This technical paper describes a software package (`diveMove`) I developed in the `GNU R` system to perform the diving behaviour analyses throughout this dissertation. This software package is freely and publicly available.

Diving Behaviour Analysis in R

An Introduction to the diveMove Package

by Sebastián P. Luque

Introduction

Remarkable developments in technology for electronic data collection and archival have increased researchers' ability to study the behaviour of aquatic animals while reducing the effort involved and impact on study animals. For example, interest in the study of diving behaviour led to the development of minute time-depth recorders (TDRs) that can collect more than 15 MB of data on depth, velocity, light levels, and other parameters as animals move through their habitat. Consequently, extracting useful information from TDRs has become a time-consuming and tedious task. Therefore, there is an increasing need for efficient software to automate these tasks, without compromising the freedom to control critical aspects of the procedure.

There are currently several programs available for analyzing TDR data to study diving behaviour. The large volume of peer-reviewed literature based on results from these programs attests to their usefulness. However, none of them are in the free software domain, to the best of my knowledge, with all the disadvantages it entails. Therefore, the main motivation for writing **diveMove** was to provide an R package for diving behaviour analysis allowing for more flexibility and access to intermediate calculations. The advantage of this approach is that researchers have all the elements they need at their disposal to take the analyses beyond the standard information returned by the program.

The purpose of this article is to outline the functionality of **diveMove**, demonstrating its most useful features through an example of a typical diving behaviour analysis session. Further information can be obtained by reading the vignette that is included in the package (`vignette("diveMove")`) which is currently under development, but already shows basic usage of its main functions. **diveMove** is available from CRAN, so it can easily be installed using `install.packages()`.

The diveMove Package

diveMove offers functions to perform the following tasks:

- Identification of wet vs. dry periods, defined by consecutive readings with or without depth measurements, respectively, lasting more than a user-defined threshold. Depending on the sampling protocol programmed in the instrument, these correspond to wet vs. dry periods, respectively. Each period is individually identified for later retrieval.
- Calibration of depth readings, which is needed to correct for shifts in the pressure transducer. This can be done using a **tcltk** graphical user interface (GUI) for chosen periods in the record, or by providing a value determined a priori for shifting all depth readings.
- Identification of individual dives, with their different phases (descent, bottom, and ascent), using various criteria provided by the user. Again, each individual dive and dive phase is uniquely identified for future retrieval.
- Calibration of speed readings using the method described by Blackwell et al. (1999), providing a unique calibration for each animal and deployment. Arguments are provided to control the calibration based on given criteria. Diagnostic plots can be produced to assess the quality of the calibration.
- Summary of time budgets for wet vs. dry periods.
- Dive statistics for each dive, including maximum depth, dive duration, bottom time, post-dive duration, and summaries for each dive phases, among other standard dive statistics.
- **tcltk** plots to conveniently visualize the entire dive record, allowing for zooming and panning across the record. Methods are provided to include the information obtained in the points above, allowing the user to quickly identify what part of the record is being displayed (period, dive, dive phase).

Additional features are included to aid in analysis of movement and location data, which are often collected concurrently with TDR data. They include calculation of distance and speed between successive locations, and filtering of erroneous locations using various methods. However, **diveMove** is primarily a diving behaviour analysis package, and other packages are available which provide more extensive animal movement analysis features (e.g. **trip**).

The tasks described above are possible thanks to the implementation of three formal S4 classes to represent TDR data. Classes `TDR` and `TDRspeed` are used to represent data from TDRs with and without speed sensor readings, respectively. The latter class inherits from the former, and other concurrent data can be included with either of these objects. A third formal class (`TDRcalibrate`) is used to represent data obtained during the various intermediate steps described above. This structure greatly facilitates the retrieval of useful information during analyses.

Data Preparation

TDR data are essentially a time-series of depth readings, possibly with other concurrent parameters, typically taken regularly at a user-defined interval. Depending on the instrument and manufacturer, however, the files obtained may contain various errors, such as repeated lines, missing sampling intervals, and invalid data. These errors are better dealt with using tools other than R, such as `awk` and its variants, because such stream editors use much less memory than R for this type of problems, especially with the typically large files obtained from TDRs. Therefore, **diveMove** currently makes no attempt to fix these errors. Validity checks for the TDR classes, however, do test for time series being in increasing order.

Most TDR manufacturers provide tools for downloading the data from their TDRs, but often in a proprietary format. Fortunately, some of these manufacturers also offer software to convert the files from their proprietary format into a portable format, such as comma-separated-values (csv). At least one of these formats can easily be understood by R, using standard functions, such as `read.table()` or `read.csv()`. **diveMove** provides constructors for its two main formal classes to read data from files in one of these formats, or from simple data frames.

How to Represent TDR Data?

`TDR` is the simplest class of objects used to represent TDR data in **diveMove**. This class, and its `TDRspeed` subclass, stores information on the source file for the data, the sampling interval, the time and depth readings, and an optional data frame containing additional parameters measured concurrently. The only difference between `TDR` and `TDRspeed` objects is that the latter ensures the presence of a speed vector in the data frame with concurrent measurements. These classes have the following slots:

file: character,

dtime: numeric,

time: POSIXct,

depth: numeric,

concurrentData: data.frame

Once the TDR data files are free of errors and in a portable format, they can be read into a data frame, using e.g.:

```
R> ff <- system.file(file.path("data",
+     "dives.csv"), package = "diveMove")
R> tdrXcsv <- read.csv(ff)
```

and then put into one of the `TDR` classes using the function `createTDR()`. Note, however, that this approach requires knowledge of the sampling interval and making sure that the data for each slot are valid:

```
R> library("diveMove")
R> ddtt.str <- paste(tdrXcsv$date,
+     tdrXcsv$time)
R> ddtt <- strptime(ddtt.str,
+     format = "%d/%m/%Y %H:%M:%S")
R> time.posixct <- as.POSIXct(ddtt,
+     tz = "GMT")
R> tdrX <- createTDR(time = time.posixct,
+     depth = tdrXcsv$depth,
+     concurrentData = tdrXcsv[,
+         -c(1:3)], dtime = 5,
+     file = ff)
R> tdrX <- createTDR(time = time.posixct,
+     depth = tdrXcsv$depth,
+     concurrentData = tdrXcsv[,
+         -c(1:3)], dtime = 5,
+     file = ff, speed = TRUE)
```

If the files are in *.csv format, these steps can be automated using the `readTDR()` function to create an object of one of the formal classes representing TDR data (`TDRspeed` in this case), and immediately begin using the methods provided:

```
R> tdrX <- readTDR(ff, speed = TRUE)
R> plotTDR(tdrX)
```

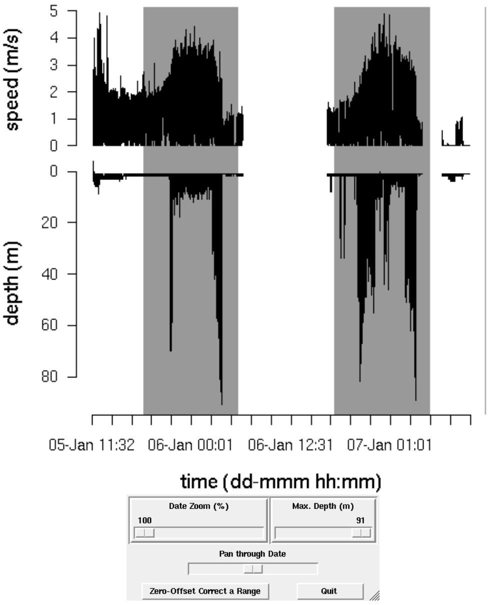

Figure 1: The `plotTDR()` method for `TDR` objects produces an interactive plot of the data, allowing for zooming and panning.

Several arguments for `readTDR()` allow mapping of data from the source file to the different slots in `diveMove`'s classes, the time format in the input and the time zone attribute to use for the time readings.

Various methods are available for displaying TDR objects, including `show()`, which provides an informative summary of the data in the object, extractors and replacement methods for all the slots. There is a `plotTDR()` method (Figure 1) for both `TDR` and `TDRspeed` objects. The `interact` argument allows for suppression of the **tcltk** interface. Information on these methods is available from `methods?TDR`.

`TDR` objects can easily be coerced to data frame (`as.data.frame()` method), without losing information from any of the slots. `TDR` objects can additionally be coerced to `TDRspeed`, whenever it makes sense to do so, using an `as.TDRspeed()` method.

Identification of Activities at Various Scales

One the first steps of dive analysis involves correcting depth for shifts in the pressure transducer, so that surface readings correspond to zero. Such shifts are usually constant for an entire deployment period, but there are cases where the shifts vary within a particular deployment, so shifts remain difficult to detect and dives are often missed. Therefore, a visual examination of the data is often the only way to detect the location and magnitude of the shifts. Visual adjustment for shifts in depth readings is tedious, but has many advantages which may save time during later stages of analysis. These advantages include increased understanding of the data, and early detection of obvious problems in the records, such as instrument malfunction during certain intervals, which should be excluded from analysis.

Zero-offset correction (ZOC) is done using the function `zoc()`. However, a more efficient method of doing this is with function `calibrateDepth()`, which takes a `TDR` object to perform three basic tasks. The first is to ZOC the data, optionally using the **tcltk** package to be able to do it interactively:

```
R> dcalib <- calibrateDepth(tdrX)
```

This command brings up a plot with **tcltk** controls allowing to zoom in and out, as well as pan across the data, and adjust the `depth` scale. Thus, an appropriate time window with a unique surface depth value can be displayed. This allows the user to select a `depth` scale that is small enough to resolve the surface value using the mouse. Clicking on the ZOC button waits for two clicks: i) the coordinates of the first click define the starting time for the window to be ZOC'ed, and the depth corresponding to the surface, ii) the second click defines the end time for the window (i.e. only the x coordinate has any meaning). This procedure can be repeated as many times as needed. If there is any overlap between time windows, then the last one prevails. However, if the offset is known a priori, there is no need to go through all this procedure, and the value can be provided as the argument `offset` to `calibrateDepth()`. For example, preliminary inspection of object `tdrX` would have revealed a 3 m offset, and we could have simply called (without plotting):

```
R> dcalib <- calibrateDepth(tdrX,
+     offset = 3)
```

Once depth has been ZOC'ed, the second step `calibrateDepth()` will perform is identify dry and wet periods in the record. Wet periods are those with depth readings, dry periods are those without them. However, records may have aberrant missing depth that should not define dry periods, as they are usually of very short duration[1]. Likewise, there may be periods of wet activity that are too short to be compared with other wet periods, and need to be excluded from further analyses. These aspects can be controlled by setting the arguments `dry.thr` and `wet.thr` to appropriate values.

Finally, `calibrateDepth()` identifies all dives in the record, according to a minimum depth criterion given as its `dive.thr` argument. The value for this criterion is typically determined by the resolution of the instrument and the level of noise close to the surface. Thus, dives are defined as departures from the surface to maximal depths below `dive.thr` and the subsequent return to the surface. Each dive may subsequently be referred to by an integer number indicating its position in the time series.

Dive phases are also identified at this last stage. Detection of dive phases is controlled by three arguments: a critical quantile for rates of vertical descent (`descent.crit.q`), a critical quantile for rates of ascent (`ascent.crit.q`), and a proportion of maximum depth (`wiggle.tol`). The first two arguments are used to define the rate of descent below which the descent phase is deemed to have ended, and the rate of ascent above which the ascent phases is deemed to have started, respectively. The rates are obtained from all successive rates of vertical movement from the surface to the first (descent) and last (ascent) maximum dive depth. Only positive rates are considered for the descent, and only negative rates are considered for the ascent. The purpose of this restriction is to avoid having any reversals of direction or histeresis events resulting in phases determined exclusively by those events. The `wiggle.tol` argument determines the proportion of maximum dive depth above which wiggles are not allowed to terminate descent, or below which they should be considered as part of the bottom phase.

---

[1] They may result from animals resting at the surface of the water long enough to dry the sensors.

A more refined call to `calibrateDepth()` for object `tdrX` may be:

```
R> dcalib <- calibrateDepth(tdrX,
+     offset = 3, wet.thr = 70,
+     dry.thr = 3610, dive.thr = 4,
+     descent.crit.q = 0.1,
+     ascent.crit.q = 0.1, wiggle.tol = 0.8)
```

The result (value) of this function is an object of class `TDRcalibrate`, where all the information obtained during the tasks described above are stored.

How to Represent Calibrated TDR Data?

Objects of class TDRcalibrate contain the following slots, which store information during the major procedures performed by `calibrateDepth()`:

tdr: `TDR`. The object which was calibrated.

gross.activity: `list`. This list contains four components with details on wet/dry activities detected, such as start and end times, durations, and identifiers and labels for each activity period. Five activity categories are used for labelling each reading, indicating dry (L), wet (W), underwater (U), diving (D), and brief wet (Z) periods. However, underwater and diving periods are collapsed into wet activity at this stage (see below).

dive.activity: `data.frame`. This data frame contains three components with details on the diving activities detected, such as numeric vectors identifying to which dive and post-dive interval each reading belongs to, and a factor labelling the activity each reading represents. Compared to the `gross.activity` slot, the underwater and diving periods are discerned here.

dive.phases: `factor`. This identifies each reading with a particular dive phase. Thus, each reading belongs to one of descent, descent/bottom, bottom, bottom/ascent, and ascent phases. The descent/bottom and bottom/ascent levels are useful for readings which could not unambiguously be assigned to one of the other levels.

dry.thr: `numeric`.

wet.thr: `numeric`.

dive.thr: `numeric`. These last three slots store information given as arguments to `calibrateDepth()`, documenting criteria used during calibration.

speed.calib.coefs: `numeric`. If the object calibrated was of class `TDRspeed`, then this is a vector of length 2, with the intercept and the slope of the speed calibration line (see below).

All the information contained in each of these slots is easily accessible through extractor methods for objects of this class (see class?TDRcalibrate). An appropriate `show()` method is available to display a short summary of such objects, including the number of dry and wet periods identified, and the number of dives detected.

The `TDRcalibrate` `plotTDR()` method for these objects allows visualizing the major wet/dry activities throughout the record (Figure 2):

```
R> plotTDR(dcalib, concurVars = "light",
+     concurVarTitles = c("speed (m/s)",
+         "light"), surface = TRUE)
```

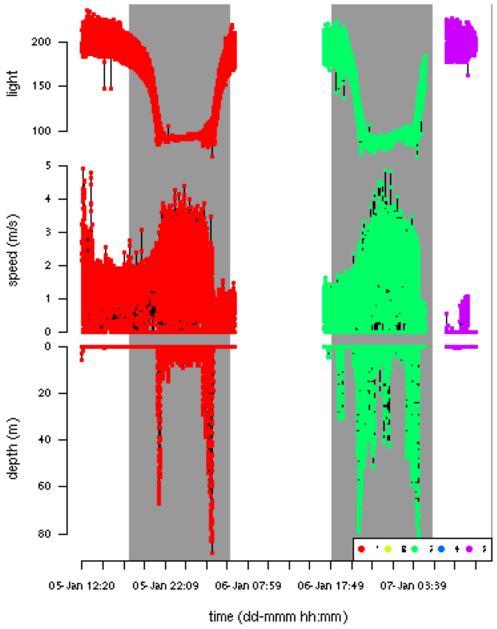

Figure 2: The `plotTDR()` method for `TDRcalibrate` objects displays information on the major activities identified throughout the record (wet/dry periods here).

The `dcalib` object contains a `TDRspeed` object in its `tdr` slot, and speed is plotted by default in this case. Additional measurements obtained concurrently can also be plotted using the `concurVars` argument. Titles for the depth axis and the concurrent parameters use separate arguments; the former uses `ylab.depth`, while the latter uses `concurVarTitles`. Convenient default values for these are provided. The `surface` argument controls whether post-dive readings should be plotted; it is `FALSE` by default, causing only dive readings to be plotted which saves time plotting and re-plotting the data. All plot methods use the underlying `plotTD()` function, which has other useful arguments that can be passed from these methods.

A more detailed view of the record can be obtained by using a combination of the `diveNo` and the `labels` arguments to this plotTDR() method. This is useful if, for instance, closer inspection of certain dives is needed. The following call displays a plot of dives 2 through 8 (Figure 3):

```
R> plotTDR(dcalib, diveNo = 2:8,
+      labels = "dive.phase")
```

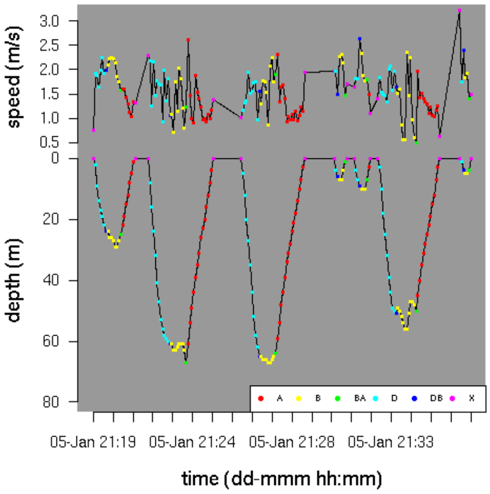

Figure 3: The `plotTDR()` method for `TDRcalibrate` objects can also display information on the different activities during each dive record (descent=D, descent/bottom=DB, bottom=B, bottom/ascent=BA, ascent=A, X=surface).

The `labels` argument allows the visualization of the identified dive phases for all dives selected. The same information can also be obtained with the `extractDive()` method for TDRcalibrate objects:

```
R> extractDive(dcalib, diveNo = 2:8)
```

Other useful extractors include: `getGAct()` and `getDAct()`. These methods extract the whole `gross.activity` and `dive.activity`, respectively, if given only the `TDRcalibrate` object, or a particular component of these slots, if supplied a string with the name of the component. For example: `getGAct(dcalib, "trip.act")` would retrieve the factor identifying each reading with a wet/dry activity and `getDAct(dcalib, "dive.activity")` would retrieve a more detailed factor with information on whether the reading belongs to a dive or a brief aquatic period.

With the information obtained during this calibration procedure, it is possible to calculate dive statistics for each dive in the record.

Dive Summaries

A table providing summary statistics for each dive can be obtained with the function `diveStats()` (Figure 4).

`diveStats()` returns a data frame with the final summaries for each dive (Figure 4), providing the following information:

- The time of start of the dive, the end of descent, and the time when ascent began.
- The total duration of the dive, and that of the descent, bottom, and ascent phases.
- The vertical distance covered during the descent, the bottom (a measure of the level of "wiggling", i.e. up and down movement performed during the bottom phase), and the vertical distance covered during the ascent.
- The maximum depth attained.
- The duration of the post-dive interval.

A summary of time budgets of wet vs. dry periods can be obtained with `timeBudget()`, which returns a data frame with the beginning and ending times for each consecutive period (Figure 4). It takes a `TDRcalibrate` object and another argument (`ignoreZ`) controlling whether aquatic periods that were briefer than the user-specified threshold[2] should be collapsed within the enclosing period of dry activity.

These summaries are the primary goal of **diveMove**, but they form the basis from which more elaborate and customized analyses are possible, depending on the particular research problem. These include investigation of descent/ascent rates based on the depth profiles, and bout structure analysis. Some of these will be implemented in the future.

In the particular case of `TDRspeed` objects, however, it may be necessary to calibrate the speed readings before calculating these statistics.

Calibrating Speed Sensor Readings

Calibration of speed sensor readings is performed using the procedure described by Blackwell et al. (1999). Briefly the method rests on the principle that for any given rate of depth change, the lowest measured speeds correspond to the steepest descent angles, i.e. vertical descent/ascent. In this case, measured speed and rate of depth change are expected to be equal. Therefore, a line drawn through the bottom edge of the distribution of observations in a plot of measured speed vs. rate of depth change would provide a calibration line. The calibrated speeds, therefore, can be calculated by reverse estimation of rate of depth change from the regression line.

---

[2] This corresponds to the value given as the `wet.thr` argument to `calibrateDepth()`.

```
R> tdrXSumm1 <- diveStats(dcalib)
R> names(tdrXSumm1)

 [1] "begdesc"            "enddesc"            "begasc"             "desctim"
 [5] "botttim"            "asctim"             "descdist"           "bottdist"
 [9] "ascdist"            "desc.tdist"         "desc.mean.speed"    "desc.angle"
[13] "bott.tdist"         "bott.mean.speed"    "asc.tdist"          "asc.mean.speed"
[17] "asc.angle"          "divetim"            "maxdep"             "postdive.dur"
[21] "postdive.tdist"     "postdive.mean.speed"

R> tbudget <- timeBudget(dcalib, ignoreZ = TRUE)
R> head(tbudget, 4)

  phaseno activity                 beg                 end
1       1        W 2002-01-05 11:32:00 2002-01-06 06:30:00
2       2        L 2002-01-06 06:30:05 2002-01-06 17:01:10
3       3        W 2002-01-06 17:01:15 2002-01-07 05:00:30
4       4        L 2002-01-07 05:00:35 2002-01-07 07:34:00

R> trip.labs <- stampDive(dcalib, ignoreZ = TRUE)
R> tdrXSumm2 <- data.frame(trip.labs, tdrXSumm1)
R> names(tdrXSumm2)

 [1] "trip.no"            "trip.type"          "beg"                "end"
 [5] "begdesc"            "enddesc"            "begasc"             "desctim"
 [9] "botttim"            "asctim"             "descdist"           "bottdist"
[13] "ascdist"            "desc.tdist"         "desc.mean.speed"    "desc.angle"
[17] "bott.tdist"         "bott.mean.speed"    "asc.tdist"          "asc.mean.speed"
[21] "asc.angle"          "divetim"            "maxdep"             "postdive.dur"
[25] "postdive.tdist"     "postdive.mean.speed"
```

Figure 4: Per-dive summaries can be obtained with functions `diveStats()`, and a summary of time budgets with `timeBudget()`. `diveStats()` takes a `TDRcalibrate` object as a single argument (object `dcalib` above, see text for how it was created).

diveMove implements this procedure with function `calibrateSpeed()`. This function performs the following tasks:

1. Subset the necessary data from the record. By default only data corresponding to depth changes > 0 are included in the analysis, but higher constraints can be imposed using the `z` argument. A further argument limiting the data to be used for calibration is `bad`, which is a vector with the minimum **rate** of depth change and minimum speed readings to include in the calibration. By default, values > 0 for both parameters are used.
2. Calculate the binned bivariate kernel density and extract the desired contour. Once the proper data were obtained, a bivariate normal kernel density grid is calculated from the relationship between measured speed and rate of depth change (using the **KernSmooth** package). The choice of bandwidths for the binned kernel density is made using `bw.nrd`. The `contour.level` argument to `calibrateSpeed()` controls which particular contour should be extracted from the density grid. Since the interest is in defining a regression line passing through the lower densities of the grid, this value should be relatively low (it is set to 0.1 by default).
3. Define the regression line passing through the lower edge of the chosen contour. A quantile regression through a chosen quantile is used for this purpose. The quantile can be specified using the `tau` argument, which is passed to the rq() function in package **quantreg**. `tau` is set to 0.1 by default.
4. Finally, the speed readings in the `TDR` object are calibrated.

As recognized by Blackwell et al. (1999), the advantage of this method is that it calibrates the instrument based on the particular deployment conditions (i.e. controls for effects of position of the instrument on the animal, and size and shape of the instrument, relative to the animal's morphometry, among others). However, it is possible to supply the coefficients of this regression if they were estimated separately; for instance, from an experiment. The argument `coefs` can be used for this purpose, which is then assumed to contain the intercept and the slope of the line. `calibrateSpeed()` returns a `TDRcalibrate` object, with calibrated speed readings included in its `tdr` slot, and the coefficients used for calibration.

For instance, to calibrate speed readings using the 0.1 quantile regression of measured speed vs. rate of depth change, based on the 0.1 contour of the bivariate kernel densities, and including only changes in depth > 1, measured speeds and rates of depth change > 0:

```
R> vcalib <- calibrateSpeed(dcalib,
+      tau = 0.1, contour.level = 0.1,
+      z = 1, bad = c(0, 0),
+      cex.pts = 0.2)
```

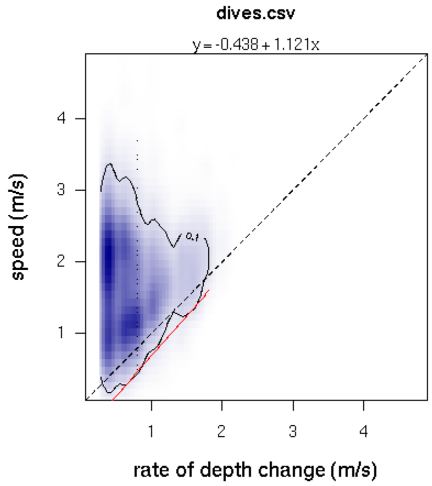

Figure 5: The relationship between measured speed and rate of depth change can be used to calibrate speed readings. The line defining the calibration for speed measurements passes through the bottom edge of a chosen contour, extracted from a bivariate kernel density grid.

This call produces the plot shown in Figure 5, which can be suppressed by the use of the logical argument `plot`. Calibrating speed readings allows for the meaningful interpretation of further parameters calculated by `diveStats()`, whenever a `TDRspeed` object was found in the `TDRcalibrate` object:

- The total distance travelled, mean speed, and diving angle during the descent and ascent phases of the dive.
- The total distance travelled and mean speed during the bottom phase of the dive, and the post-dive interval.

Summary

The **diveMove** package provides tools for analyzing diving behaviour, including convenient methods for the visualization of the typically large amounts of data collected by TDRs. The package's main strengths are its ability to:

1. identify wet vs. dry periods,
2. calibrate depth readings,
3. identify individual dives and their phases,
4. summarize time budgets,
5. calibrate speed sensor readings, and
6. provide basic summaries for each dive identified in TDR records.

Formal S4 classes are supplied to efficiently store TDR data and results from intermediate analysis, making the retrieval of intermediate results readily available for customized analysis. Development of the package is ongoing, and feedback, bug reports, or other comments from users are very welcome.

Acknowledgements

Many of the ideas implemented in this package developed over fruitful discussions with my mentors John P.Y. Arnould, Christophe Guinet, and Edward H. Miller. I would like to thank Laurent Dubroca who wrote draft code for some of **diveMove**'s functions. I am also greatly endebted to the regular contributors to the R-help newsgroup who helped me solve many problems during development.

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B At-sea distribution of adult females

This publication compares the general distribution of adult females of Antarctic and subantarctic fur seals equipped at Ile de la Possession during the 2002 and 2003 study periods. The idea for the study developed from my initial Ph.D. research programme proposal. In addition to the initial idea for the study, I participated in all field activities, and provided suggestions for analyses on diving behaviour.

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Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands

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ABSTRACT: Marine top-predators such as marine mammals forage in a heterogeneous environment according to their energetic requirements and to the variation in environmental characteristics. In this study, the behaviour of breeding females in 2 sympatric fur seal species, Antarctic fur seal *Arctocephalus gazella* and Subantarctic fur seal *A. tropicalis*, was investigated in relation to foraging effort. Foraging effort was hypothesised to be greater in Antarctic fur seal than in Subantarctic fur seal due to their shorter lactation period. Using satellite telemetry, time-depth recorders and satellite images of sea-surface temperature and chlorophyll *a* concentration, the foraging grounds, the at-sea activity budgets and the environmental features were determined for both species breeding on the Crozet Archipelago. Foraging cycle duration was similar for the 2 species, and the seals exhibited similar at-sea activity budgets. Only the proportion of time spent at sea was higher in Antarctic fur seals. Separate foraging areas were identified for the 2 species. Antarctic fur seal distribution was related to bathymetric features, while we did not find any direct relationship between chlorophyll *a* concentration and seal foraging areas. Our results suggest that Antarctic fur seals tend to respond to the higher needs of their pups by having a higher foraging efficiency and concentrating their foraging activity in the most productive areas.

KEY WORDS: Activity budget · Spatial distribution · Environmental features · Otariidea · *Arctocephalus gazella* · *Arctocephalus tropicalis*

INTRODUCTION

The foraging behaviours of marine mammals are related to the energetic requirements of individuals and environmental characteristics (McCafferty et al. 1998, Costa & Gales 2003). Indeed, according to optimal foraging theory (McArthur & Pianka 1966), organisms are supposed to adopt foraging behaviours that optimise fitness for given environmental conditions. These determine how, when and where each animal acquires its food. More precisely, in a 'patchy habitat', according to the marginal-value theorem (Charnov 1976), a predator must make decisions as to which patch types it will visit and when it will leave the patch.

In the marine environment, food resources are distributed heterogeneously in space and time and their distribution is generally related to the heterogeneity in oceanographic features (Pakhomov & McQuaid 1996, Loeb et al. 1997, Guinet et al. 2001). Distribution and behaviour of top marine predators are related to physical and biological features (bathymetry, sea-surface temperature, primary productivity), as found in seabirds (Bost et al. 1997, Guinet et al. 1997, Weimerskirch 1998) and pinnipeds (Boyd et al. 1998, Georges et al. 2000). Resources are also limited in space and time. If 2 species exploit the same ecological niche and if the resources are limited, ecological segregation resulting from competition between these species should

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inevitably take place (Hutchinson 1957). So sympatric species must have different ecological functions in the ecosystem in order to coexist.

During the breeding season there is a double problem for marine predators: to obtain food for themselves and their offspring. Furthermore, during the breeding period, seabirds and otariids are central-place foragers (Orians & Pearson 1979), alternating between periods of foraging at sea and feeding their chicks or suckling their pups on land (Bonner 1984, Gentry & Kooyman 1986). The behaviours adopted by parents are spatially and temporally limited to avoid progeny starvation. Therefore, time and energetic expenditure are the 2 principal constraints for central-place foragers during the breeding season (Ydenberg et al. 1994, Houston 1995).

Among pinnipeds, otariids have the longest lactation period, but with a large degree of variation in its duration. Generally, species that breed at temperate latitudes, like the New Zealand fur seals *Arctocephalus forsteri*, Juan Fernandez fur seals *A. philipii*, South African fur seals *A. pusillus* or Subantarctic fur seals *A. tropicalis*, suckle their pup for 10 mo, while the Alaskan fur seals *Callorhinus ursinus* and the Antarctic fur seals *A. gazella*, which breed in high latitudes and productive water, raise their pups over a 4 mo lactation period (Gentry & Kooyman 1986).

Two species that display markedly different lactation lengths, Antarctic fur seal and Subantarctic fur seal, breed sympatrically on the Crozet Archipelago. At weaning, the size and the body mass of pups of the 2 species are identical (S. Luque unpubl. data), but a previous study showed that in-air resting metabolic rates (RMR) and daily energy expenditure (DEE) were higher in Antarctic fur seal pups than in similar-aged Subantarctic fur seals at Crozet (Arnould et al. 2003). These observations corroborate observations that Antarctic fur seal pups spend more time swimming than in similar-aged Subantarctic fur seal pups (S. Luque, J. P. Y. Arnould & C. Guinet unpubl. data). We, therefore, hypothesised that Antarctic fur seal females have to expend a higher foraging effort or forage more efficiently to acquire more resources at sea to cover the higher needs of their pups compared to Subantarctic fur seal females. However, amongst marine mammals, the foraging efficiency of parents is not easy to measure, because it is difficult to assess precisely the amount of energy acquired in relation to the energy spent by the female to acquire that energy. One means of evaluating foraging effort is to use the time budget as a proxy of energy expenditure (Arnould & Boyd 1996, Boyd 1999).

Both species have been studied at their allopatric sites, revealing a variety of foraging behaviours. For example, very long trips (maximum distance from the colony > 100 km) were recorded for Subantarctic fur seals from Amsterdam Island (Georges et al. 2000, Beauplet et al. 2004). Similarly, an important variability in the diving activity of Antarctic fur seals was observed at the Kerguelen Islands (Bonadonna et al. 2000, Lea et al. 2002). The sympatric populations of Antarctic fur seals and Subantarctic fur seals at Crozet Island, like at Marion Island (Kerley 1985) and Macquarie Island (Robinson et al. 2002), allow comparisons of the foraging behaviour between 2 taxonomically similar species with different breeding strategies but under identical environmental conditions. The aim of this paper was (1) to investigate the spatial segregation and foraging behaviours of sympatric lactating female Antarctic and Subantarctic fur seals at Crozet and (2) to uncover new aspects of the relationship between foraging behaviours and energy expenditure.

MATERIALS AND METHODS

Study area and seals. The study was conducted in the Crozet Islands, an archipelago in the Southern Indian Ocean, during the austral summers 2001/2002 and 2002/2003 (December to March). La Mare aux Elephants (46.37° S, 51.69° E), north-west of Possession Island, accommodates 1 breeding colony. Each species, Antarctic fur seal *Arctocephalus gazella* and Subantarctic fur seal *Arctocephalus tropicalis*, has different preferred substrate types, beaches for Antarctic fur seals and rock platforms and large boulders for Subantarctic fur seals, but they breed within a few metres of each other. Population growth rates for both Antarctic and Subantarctic fur seals on this island are currently ~18 % per annum (Guinet et al. 1994, C. Guinet unpubl. data). Annual pup productions at La Mare aux Elephants were 164 for Antarctic fur seals and 80 for Subantarctic fur seals in 2001/2002.

Capture and device attachment. Lactating female fur seals of both species were instrumented. Individuals were selected randomly, captured using a hoop net, weighed and restrained for up to 20 min on a restraining board while the devices were attached. At-sea behaviour was investigated using several loggers described in Table 1. Time-depth recorders (MK7 TDR, Wildlife Computers) were mounted on a satellite transmitter (platform terminal transmitter [PTT], Sirtack New Zealand, Telonics) in all cases. The larger size of the velocity-time-depth recorders (MK8 TDR, Wildlife Computers) precluded simultaneous deployment of an additional PTT. The package (MK7 + PTT) was shaped to minimise drag and was attached, like the MK8, with plastic cable ties to a nylon webbing strap that was glued on the dorsal midline between the scapulae of each animal with double component araldite glue

Table 1. Features of logger used (x indicates that the parameter is present or measured)

Devices			Physical features			Parameters measured and used in this study				Configuration
Generic name	Type	Memory	Dimensions (mm)	Weight (g)	Cross-sectional area (cm^2)	Pressure (depth)	Speed of swim	Sensor 'wet-dry'	Location (lat.–long.)	Record interval
Time depth recorder	TDR MK7	x	90 × 20 × 10	30	2.2	Resolution (1 m)		x		5 s
Time depth recorder	TDR MK8	x	80 × 50 × 30	100	8	Resolution (1 m)	Resolution (0.1 m s^{-1})	x		5 s
Satellite Argos system	PTT 100		110 × 42 × 14	120	5.7				x	

(AW 2101, Ciba Speciality Chemicals). The seals were recaptured after 1 to 3 consecutive foraging trips (the trip duration ranged from 2.5 h to 6.5 d). Devices were removed by cutting the fur underneath with a scalpel blade and subsequently deployed on different individuals. Individual devices were deployed alternately on the 2 species.

Activity budgets. The MK7 TDRs measured wet and dry periods and depth (±1 m) every 5 s with a pre-calibrated pressure transducer. The MK8 TDRs also measured speed, with a pre-calibrated rotating turbine. The downloaded hexadecimal TDR files were converted into binary files using 'Hex Decoder' software (Wildlife Computers). Data were used to estimate the foraging-trip composition of the seals. We defined a foraging cycle (FC) as a trip to sea plus the subsequent period on land. In order to exclude short bathing periods undertaken by females during the suckling period on land, an individual was considered to undertake a foraging trip when at sea for >1 h.

The at-sea activity budget was calculated for each complete foraging trip recorded for each seal equipped with a MK8 TDR and defined as the amount of time dedicated to diving, travelling and resting. Diving activity was defined when depth was >4 m (Lea et al. 2002). Travelling activity was defined when depth was <4 m and speed was >0, while resting corresponded to the period in which fur seals were not diving and when speed equalled 0. All data manipulations and statistical analyses were conducted using R software (Ihaka & Gentleman 1996).

The average swimming velocity, obtained from the MK8 data, was first compared between global foraging trips and next just on a section of a trip, where fur seals travelled regularly (Bonadonna et al. 2000). Therefore, a possible difference in the diving speed can be deduced.

Satellite transmitters and spatial distribution. PTT locations were calculated by reference to 3 satellites and assigned by the Argos system (Toulouse, France) to 6 classes on the basis of their estimated accuracy. The accuracy of locations provided by Argos is classified as follows: Class 3 is accurate to 150 m; Class 2, to 350 m; Class 1, to 1 km; and Classes 0, A and B have no accuracy assigned. Only 5 classes (A, 0, 1, 2, 3), allowing the location of animals with an error margin of <4.5 ± 5.9 km (Bonadonna et al. 2000), were included in these analyses. Data were plotted using Elsa99 software (release 1.0, Soft & Technique Informatique). Locations were filtered such that those that suggested transit speeds >3 m s^{-1} were excluded (Weimerskirch et al. 1995, Bost et al. 1997, Boyd et al. 1998, Bonadonna et al. 2000). The maximal distance from the colony reached by each seal was measured between the farthest point and the colony, and the total length of a foraging trip was obtained by summing all distances between 2 consecutive points of this trip. We also calculated a curvilinear index to determine the shape of each trip. Indeed, with this index, it was possible to determine whether the seal went to the foraging area directly or using a loop like some marine birds (Weimerskirch et al. 1993). The index was calculated by the following formula:

$$s = (2 \times \text{maximal distance})/(\text{total length of trip})$$

The closer this index is to 1 the more direct the trip is.

Females of the 2 species dive almost exclusively at night at Crozet (87 and 89 % of dives occurred at night for Antarctic and Subantarctic fur seals, respectively (S. Luque unpubl. data). This result is coherent with diving behaviour of most fur seal species (Gentry & Kooyman 1986, Goldworthy et al. 1997). As a result, only at-sea, night-time locations were used to evaluate the spatial distribution of foraging ground for both species. To determine the accurate limits of the night, we consulted a sun time table (suntab.exe software, www.cafe.rapidus.net/sbelange/logiciel.html). Moreover, to avoid problems of independence of the data, only 1 foraging trip for each animal was used in the analyses.

In order to analyse the intensity of use of different areas within the activity range of seals, the pattern of locations (satellite fixes) must be transformed into an estimate of density. Therefore, a Kernel-based method, which transforms point distributions into density estimates (Powell 2000), was used. The treatment of data was conducted using the GIS software Arcview® (version 3.2, Esri Corporation) and 'Animal Movement' extension, v.2B (Hooge & Eichenlaub 1997, Alaska Biological Science Center, www.absc.usgs.gov/glba/gistools).

Environmental data. To investigate the relationships between the foraging areas and oceanographic features, bathymetric data (resolution of 5′ grid) were extracted from the Integrated Global Ocean Service System database (http://ingrid.ldeo.columbia.edu/SOURCES/IGOSS/). In addition, sea surface temperature (SST) and chlorophyll *a* concentration data were provided by NOAA/NASA (http://daac.gsfc. nasa.gov/oceancolor) at 4 km resolution and read by HDF view software (release 1.2, University of Illinois). These data were extracted from October 2001 to February 2002 and from October 2002 to February 2003. In addition to covering the dates of device deployment, this period covered the 2 mo prior to deployment, in order to observe the evolution of SST and chlorophyll *a*, as several studies have shown that time lags may result in a lag between the distribution of primary production and top predators (Runge 1988, Jaquet et al. 1995, Lehodey et al. 1998).

Statistical analysis. Some data were discarded due to TDR dysfunction or breakdown. A synthesis of the number of individuals equipped and the number used in the analysis is presented in Table 2. Parametric test application conditions were verified using a Kolmogorov–Smirnov test and a variance-equality test. If these conditions were not verified, data were transformed to use parametrics. However, when the transformation did not provide a normal distribution, we used non-parametric statistics. In the 'Results' section we have used some abbreviations for the species names: Ag = *Arctocephalus gazella* and At = *A. tropicalis*. Data are presented as means (±SE), and values were considered significant at $p < 0.05$.

RESULTS

Foraging cycles

There was no effect of the individuals on all parameters tested ($n_{Ag} = 26$, $n_{At} = 34$, $p > 0.05$ in each ANOVA). Therefore, we calculated means of all parameters for each individual. The type of logger affected trip duration ($F = 8.011$, $p < 0.01$, GLM), with animals equipped with an MK8 TDR making longer trips than animals equipped with an MK7 TDR (2.6 ± 1.6 d against 1.7 ± 1.38 d, respectively). No significant differences were found between the 2 study years, for each species and each device type ($n_{Ag} = 26$, $n_{At} = 34$, $p > 0.05$ in all *U*-tests). No effect of the month in which devices were deployed (stage of lactation) was found on any of the FC parameters investigated ($n_{Ag} = 26$, $n_{At} = 34$, $p > 0.05$ in all Kruskal-Wallis tests). Therefore, all variables of the 2 study years were pooled for further the analyses.

No differences were observed in the length of foraging cycles between the 2 species equipped with MK7, but differences were found for animals equipped with MK8 (Table 3). Either equipped with MK7 or MK8, Antarctic fur seals had longer foraging trips than Subantarctic fur seals (Table 3). Consequently, Antarctic fur seals were found to spend proportionally more time at sea and less time ashore (Fig. 1), regardless of the type of TDR used (Table 3). No relationship was found between trip duration and time spent on land for the 2 species (Ag: $r_s = -0.02$, $p = 0.90$ and At: $r_s = 0.13$, $p = 0.44$, Spearman rank correlation test).

At-sea activity budgets

The activity budget could only be calculated for females of both species equipped with MK8 TDRs. We distinguished 3 different activities at sea: diving, travel-

Table 2. Summary of deployments and data analysis. Ag = *Arctocephalus gazella*, At = *A. tropicalis*. –: no data

		PTT + TDR MK7				MK8	
		PTT		MK7			
		No. of ind. equipped	No. used in trips analysis	No. of ind. equipped	No. used in time budget analysis	No. of ind. equipped	No. used in time budget analysis
Ag	2001–2002	18	14	18	11	17	8
	2002–2003	3	–	4	4	5	3
At	2001–2002	14	10	14	12	18	15
	2002–2003	2	–	4	3	4	3
Total		**37**	**24**	**40**	**30**	**44**	**29**

Table 3. Details of activity budget (the results are means ± SD, significant results are indicated in bold. –: no data

	MK7			MK8		
	Ag, n = 15	At, n = 15	Tests	Ag, n = 11	At, n = 18	Tests
Foraging cycle (d)	3.19 ± 1.33	2.70 ± 1.67	*U* = 144 p = 0.191	4.52 ± 1.39	3.04 ± 1.66	*U* = 149 **p = 0.025**
Trip duration (d)	2.09 ± 0.98	1.40 ± 1.65	*U* = 166 **p = 0.026**	3.61 ± 1.41	1.98 ± 1.47	*U* = 154 **p = 0.013**
On land duration (d)	1.10 ± 0.58	1.30 ± 0.74	*U* = 92 p = 0.395	0.90 ± 0.74	1.05 ± 0.46	*U* = 67 p = 0.150
Proportion of time at sea (%)	64.2 ± 9.9	37.7 ± 17.8	*U* = 204 **p < 0.001**	76.1 ± 16.0	53.5 ± 18.7	*U* = 163 **p = 0.004**
Proportion of time in diving (%)	19.4 ± 12.5	18.0 ± 8.6	–	19.1 ± 10.6	18.6 ± 8.5	KS test *D* = 0.268 p = 0.695
Proportion of time in swimming (%)	–	–	–	54.0 ± 14.3	54.7 ± 8.5	
Proportion of time in resting (%)	–	–	–	26.1 ± 9.7	20.7 ± 14.2	

ling and resting. The proportions of time spent in diving, swimming and resting were identical for the 2 species (*D* = 0.268, p = 0.69, Kolmogorov-Smirnov test). During a foraging trip, the 2 species devoted 18.8%, on average, of the time to diving, 54.3%, on average, to swimming and 23.4%, on average, to resting (Table 3, Fig. 2). There were no relationships between the proportion of time spent swimming and trip duration for the 2 species (Ag: $r_s = -0.17$, p = 0.61, n = 11 and At: $r_s = -0.11$, p = 0.66, n = 18, Spearman rank correlation test), nor for the time spent diving for Antarctic fur seals ($r_s = 0.2$, p = 0.55, n = 11, Spearman rank correlation test), but this relationship tended towards significance for Subantarctic fur seals ($r_s = -0.44$, p = 0.07, n = 18, Spearman rank correlation test). In contrast, we observed a positive relationship between the proportion of time spent resting at sea and the trip duration for Subantarctic fur seals ($r_s = 0.58$, p = 0.01, n = 18, Spearman rank correlation test), but not for Antarctic fur seals ($r_s = -0.14$, p = 0.67, n = 11, Spearman rank correlation test). No differences were found in the proportion of time spent diving for females of both species equipped either an MK7 or an MK8 TDR (Table 3).

No difference was found in the overall swimming speed along a foraging trip between Antarctic fur seals (0.61 ± 0.15 m s^{-1}, n = 12) and Subantarctic fur seals (0.54 ± 0.17 m s^{-1}, n = 13; *U* = 151, p = 0.18). Moreover, no differences were found in surface swimming speeds in transit to foraging grounds (Ag: 1.32 ± 0.28 m s^{-1}, n = 12; At: 1.20 ± 0.31 m s^{-1}, n = 13; *U* = 98.5, p = 0.26). Consequently, it is very likely that no differences exist in the diving speeds.

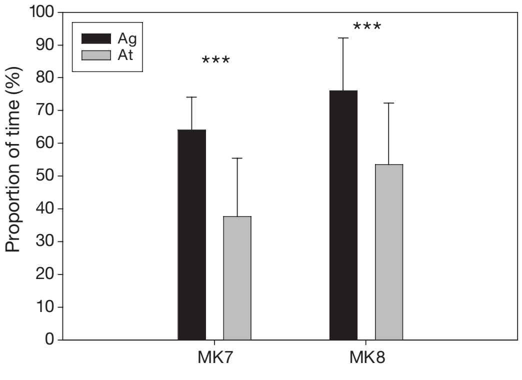

Fig. 1. *Arctocephalus gazella* (Ag), *A. tropicalis* (At). Proportion of time spent at sea during a foraging cycle (***: differences are significant at 99.9%)

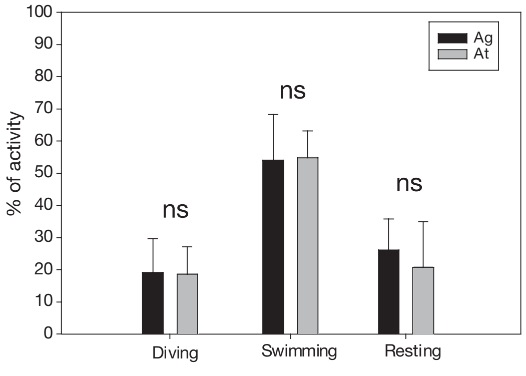

Fig. 2. *Arctocephalus gazella* (Ag), *A. tropicalis* (At). Proportion of time spent in the different activities at sea during a foraging trip (ns: differences are non-significant)

Foraging areas

PTT tags recorded 39 foraging trips (31 in 2001/2002 and 8 in 2002/2003) for 29 individuals (14 Ag and 10 At in 2001/2002 and 3 Ag and 2 At in 2002/2003) during the study period. No difference was found in the number of locations (loc.) by unit of time between the 2 species (Ag: 16.64 ± 8.22 loc. d^{-1}, n = 17; At: 14.12 ± 6.99 loc. d^{-1}, n = 12; $t = 1.135$, p = 0.27). Trips recorded were divided thus: Ag: 9 trips in December and 8 in January, and At: 4 trips in December and 8 in January. No influence of the year or of the month during which devices were deployed was found on the number of locations by day ($F = 1.183$, p = 0.35, ANCOVA).

Two particularly long trips (>500 km), 1 for each species, were removed from Kernel analysis to increase accuracy of foraging areas in 2001/2002. Because of a very low sample size obtained during the second year of the study (2002/2003), trips recorded during this period (Ag: 3 trips and At: 2 trips) were removed from analyses. No overlap was observed between the foraging distributions of the 2 species. The Antarctic fur seals concentrated foraging activity preferentially in the west of Possession Island, while the Subantarctic fur seals occupied 2 main areas in the north-west and north of the island (Fig. 3). Both species foraged over the channel separating the Possession Island shelf from Hog Island.

No significant differences were found in the total trip lengths between the 2 species (Ag: 196 ± 122 km, n = 14; At: 289 ± 239 km, n = 10; $U = 145$, p = 0.38), but the Subantarctic fur seals went farther from the colony than the Antarctic fur seals (Ag: 50 ± 27 km, n = 14; At: 95 ± 69 km, n = 10; $U = 100$, $p < 0.05$). Moreover, we found a positive relationship between total length and trip duration for the Subantarctic fur seals ($r_s = 0.905$, $p < 0.01$), but no such relationship for the Antarctic fur seals ($r_s = 0.314$, p = 0.56). Shape index indicates that the Antarctic fur seals used more trips with a loop structure compared to the Subantarctic fur seals, which used straighter trips (Ag: 0.56 ± 0.17, n = 14; At: 0.72 ± 0.18, n = 10; $U = 73$, $p < 0.01$).

The Antarctic fur seals foraged mainly over 500 to 1500 m water depth, while Subantarctic fur seals tended to forage over 2000 m water depth (Fig. 3). Monthly averages of near-surface chlorophyll *a* concentrations from October 2001 to February 2002 are presented in Fig. 3. At the scale of the Crozet Archipelago, the distribution of chlorophyll *a* concentrations, prior to and during the 2001/2002 study period, showed that most of the surface primary production took place in the northern half of this archipelago, with highest concentrations taking place in December 2001 in the area where Subantarctic fur seals concentrated their foraging activity, while the Antarctic fur seals foraged along the southern edge of the area of the maximum chlorophyll *a* concentration.

DISCUSSION

In the present study we did not compare foraging trip duration between animals equipped and unequipped, but the effect of an additional burden on the behaviour of fur seals has already been taken into account in several earlier papers (Boyd et al. 1991, 1997, Walker & Boveng 1995). However, we observed that the foraging trips of animals carrying MK8 TDRs were longer than the trips of PTT + MK7 TDR-equipped seals, suggesting MK8 TDRs affect the foraging behaviour of the seals. Bonadonna et al. (2000) found similar results. It is interesting to note that both species were affected in a similar way by MK8 TDRs compared to MK7 TDRs. Indeed, compared to females equipped with MK7 TDRs, both Antarctic and Subantarctic female fur seals (*Arctocephalus gazella*, *A. tropicalis*) equipped with MK8 TDRs exhibited an increase in their foraging trip duration, while the subsequent shore visit was unchanged. Consequently and despite similar cross-sectional areas (about 8 cm^2, see Table 1) of the 2 devices (MK8 and PTT + MK7), the proportion of time spent at sea for a foraging cycle in females of both species equipped with an MK8 TDR compared to females equipped with MK7 TDRs increased. Such consistent differences suggest that it is the hydraulic turbine of the MK8 TDRs that may be responsible for most of the drag effect during swimming compared to the other device. The biases introduced into the data are not a problem in a study that is based on the comparison between species subjected to the same treatment (MK8). Indeed, the biases are similar for the 2 species. Consequently, the conclusions would be correct in terms of the inter-specific comparison, while they should be considered more cautiously in terms of the absolute value of the foraging duration and possibly the relative percentage of activity.

Activity budget

Our results indicate that the duration of a foraging cycle and the proportion of time allocated during a foraging trip to different activities were identical among the 2 species. However, for a foraging cycle of a given duration, the at-sea part was longer for the Antarctic fur seals, resulting in a higher proportion of time spent at sea in the Antarctic fur seals compared to the Subantarctic fur seals. Indeed, over an average 3 d foraging cycle, the Antarctic female fur seals spent an aver-

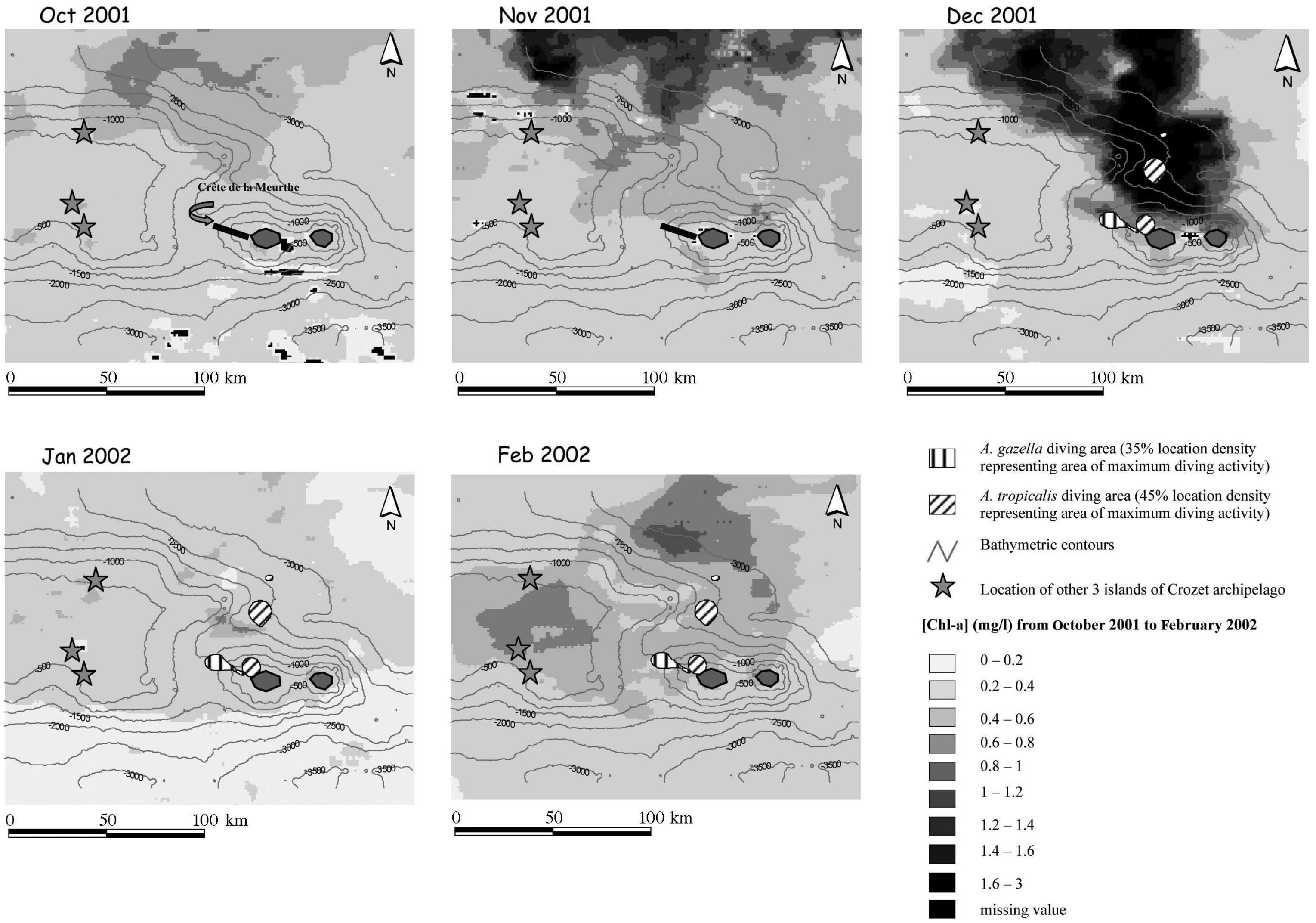

Fig. 3. *Arctocephalus gazella*, *A. tropicalis*. Evolution of chlorophyll *a* concentration and foraging grounds of female Antarctic and Subantarctic fur seals determined by a Kernel analysis of Argos data

age of 24% more time at sea, but, more importantly, 1 night longer at sea than Subantarctic female fur seals. As both species fish almost exclusively at night at Crozet, we can assume that the absolute amount of resources acquired over a foraging trip is higher in the Antarctic fur seals compared to the Subantarctic fur seals, resulting from a higher energy acquisition rate over a foraging cycle for the Antarctic fur seals than for the Subantarctic fur seals. No precise values of energetic metabolism are available for this study, but Costa et al. (1989), using the double-marked water method, measured a metabolism at sea of 9.52 W kg^{-1} for lactating females. They also found that the at-sea metabolism of the Antarctic fur seal females was only 1.9 times higher than the metabolism measured on land while fasting and lactating (Costa et al. 1989). Similar results were found for the Alaska fur seals *Callorhinus ursinus* (Costa & Gentry 1986). To our knowledge, no measurements of resting or active metabolism are available for Subantarctic fur seals. However, according to the allometric relation between the rate of base metabolism and body mass, established for pinnipeds by Lavigne et al. (1986), we can suppose that metabolism is equivalent for our 2 study models, which are taxonomically and morphologically very similar. Indeed, it is unlikely, even if there is a need to confirm this by measuring the actual metabolic rate of these 2 species at Crozet, that these species, with an identical at-sea behaviour (S. Luque unpubl. data), have very different metabolic rates. Thus, considering both identical metabolic rates at sea and on land between the 2 species, we can estimate at Crozet, due to the difference in the proportion of time spent at sea, that the Antarctic fur seals spent about 13% more energy than Subantarctic fur seals over a foraging cycle.

Arnould & Boyd (1996) found a negative relationship between the proportion of time spent diving and the at-sea metabolic rate for Antarctic fur seals at Bird Island, South Georgia. According to Butler et al. (1995), the metabolism during diving is only 20% higher than the metabolism during swimming for the Antarctic fur seal. The interpretation of Arnould & Boyd (1996) was based on the hypothesis that an animal with a higher rate of diving should spend more time resting at the surface to recover and should have a lower at-sea metabolic rate than an animal with a lower rate of diving, but spending more time swimming. However, opposite from this assumption, we found no relationship between the proportion of time spent diving and proportion of time spent resting. This result could be explained by the smaller range of trip durations sampled at Crozet Islands (2 d for both species) compared to Bird Island (4 d on average). We can therefore hypothesise that during foraging trips taking place close to the colony, as in our study, fur seals tend to come back on land to rest and suckle their pup, rather than resting at sea. The relationship between foraging trip duration and the proportion of time females spent resting and the relationship between foraging trip duration and the maximum distance from the colony support this assumption.

Foraging trip distribution in relation to oceanographic parameters

Maximum location densities were identified using the main foraging areas of the 2 species. The technique used may be biased, as the at-sea, night-time locations do not necessarily correspond to a foraging location. However, as the foraging activity is maximal at night, we can consider that these locations reveal the foraging areas of both species.

As ocean currents encounter topographic features such as seamounts, oceanic islands, or ridges, cold and deep nutrient-rich waters can be brought into the generally nutrient-poor surface water, enhancing primary production. Topographic features can also induce local aggregation of marine organisms (Lavoie et al. 2000). Advection processes would induce the aggregation process at medium to large scale, over several months, while at a smaller scale appears to result mainly from accumulation processes and behavioural and/or physiological adaptation (Mackas et al. 1985). Local aggregations are generally related to small-scale processes that are often related to a topographic change, which may indirectly act on the marine organisms.

The Subantarctic fur seals tended to forage both in an area located over the deeper water of the channel between Possession Island and Hog Island and in an area close to shore, while the Antarctic female fur seals limited their foraging to a much smaller area located on the northern edge of the 'Crête de la Meurthe', a sub-marine ridge close to Possession Island. A complementary study on the diet of the 2 species at Crozet (Y. Cherel unpubl. data) showed that the Antarctic and Subantarctic fur seals fed on the same myctophid prey organisms (principally *Gymnoscopelus* sp. and *Electrona* sp.).

The distribution of surface chlorophyll *a* over the study period indicates that the highest concentration takes place in December over that channel, and the fact that both species concentrate their foraging activity over or very close to that area from December to early March suggests that the myctophids are probably aggregated over that area in relation to some still unknown physical processes.

The absence of major differences, both in diving behaviour (S. Luque unpubl. data) and diet (Y. Cherel unpubl. data), suggests that both species are exploiting similar prey in a similar way, but in different locations. At this stage we cannot tell if this behaviour results from active competition exclusion processes and/or the selection of different qualities of foraging habitat by the 2 species. We can hypothesise that the Antarctic fur seals, which have higher needs per unit of time, could restrict their foraging behaviour to higher density prey patches, located on the northern edge of the 'Crête de la Meurthe', compared to Subantarctic fur seals, which use a less efficient foraging mode because of greater transit time (temporally shorter and spatially longer trips). Only a myctophid sampling survey like the one conducted at Kerguelen Island (Duhamel 1987, Guinet et al. 2001) will clarify these patterns.

CONCLUSIONS

Interestingly, when these 2 species are confronted with the same environmental conditions, they tend to show similar foraging behaviour, while the same species in different environments exhibit very different foraging behaviours. These observations strongly support the assertion that the foraging behaviour of fur seal species is mainly mediated by local environmental conditions.

This study also found, like another one at Macquarie Island (Robinson et al. 2002), that these sympatric fur seals exploited the marine environment in similar ways. However, the higher proportion of time spent at sea by female Antarctic fur seals compared to Subantarctic fur seals suggests that lactating female Antarctic fur seals expend more energy to acquire more energy per unit of time to match the higher energetic requirement of their pups compared to Subantarctic fur seals. This higher energy expenditure assumed in lactating female Antarctic fur seals is consistent with a shorter lactation period that still allows pups to grow to a weaning mass similar to that of Subantarctic fur seal pups over a longer lactation period.

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C Pup metabolism

This paper was prepared as a complementary, concurrent, project comparing the metabolism of pups of both species, which includes a preliminary comparison of body composition between AFS and SFS. I participated in all field activities for this study, and as second author of the paper, contributed revisions and comments on drafts during the publication process.

C Pup metabolism

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The comparative energetics and growth strategies of sympatric Antarctic and subantarctic fur seal pups at Îles Crozet

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Summary

The period of maternal dependence is a time during which mammalian infants must optimise both their growth and the development of behavioural skills in order to successfully meet the demands of independent living. The rate and duration of maternal provisioning, post-weaning food availability and climatic conditions are all factors likely to influence the growth strategies of infants. While numerous studies have documented differences in growth strategies at high taxonomic levels, few have investigated those of closely related species inhabiting similar environments. The present study examined the body composition, metabolism and indices of physiological development in pups of Antarctic fur seals (*Arctocephalus gazella*) and subantarctic fur seals (*Arctocephalus tropicalis*), congeneric species with different weaning ages (4 months and 10 months, respectively), during their overlap in lactation at a sympatric breeding site in the Iles Crozet. Body lipid reserves in pre-moult pups were significantly greater (t_{28}=2.73, P<0.01) in subantarctic (26%) than Antarctic fur seals (22%). Antarctic fur seal pups, however, had significantly higher (t_{26}=3.82, P<0.001) in-air resting metabolic rates (RMR; 17.1±0.6 ml O_2 kg^{-1} min^{-1}) than subantarctic fur seal pups (14.1±0.5 ml O_2 kg^{-1} min^{-1}). While in-water standard metabolic rate (SMR; 22.9±2.5 ml O_2 kg^{-1} min^{-1}) was greater than in-air RMR for Antarctic fur seal pups (t_9=2.59, P<0.03), there were no significant differences between in-air RMR and in-water SMR for subantarctic fur seal pups (t_{12}=0.82, P>0.4), although this is unlikely to reflect a greater ability for pre-moult pups of the latter species to thermoregulate in water. Pup daily energy expenditure was also significantly greater (t_{27}=2.36, P<0.03) in Antarctic fur seals (638±33 kJ kg^{-1} day^{-1}) than in subantarctic fur seals (533±33 kJ kg^{-1} day^{-1}), which corroborates observations that pups of the former species spend considerably more time actively learning to swim and dive. Consistent with this observation is the finding that blood oxygen storage capacity was significantly greater (t_9=2.81, P<0.03) in Antarctic (11.5%) than subantarctic fur seal (8.9%) pups. These results suggest that, compared with subantarctic fur seals, Antarctic fur seal pups adopt a strategy of faster lean growth and physiological development, coupled with greater amounts of metabolically expensive behavioural activity, in order to acquire the necessary foraging skills in time for their younger weaning age.

Key words: maternal provisioning, metabolic rate, growth strategy, resource partitioning, energetics, weaning, fur seal, *Arctocephalus gazella, Arctocephalus tropicalis.*

Introduction

Throughout the period of maternal dependence, mammalian infants must balance the demands of lean body growth, lipid storage and energy expenditure for behavioural development from the finite nutritional resources (milk or solid food) provided by their mother (Loudon and Racey, 1987; Martin, 1984; Peaker, 1989). Trade-offs, however, exist in devoting nutritional resources to various developmental pressures. For example, rapid lean growth may confer advantages to the infant in being large at weaning (e.g. enhanced defence of food resources or against predators) but limits the amount of energy that can be devoted to physical activity due to the high maintenance metabolism costs associated with a large lean body mass (Blaxter, 1989; Innes and Millar, 1995). Conversely, high levels of energy expenditure devoted to behavioural development (usually through play) may enhance hunting ability or predator avoidance but limit the storage of body lipids that could be crucial to post-weaning survival during the early period of nutritional independence when foraging efficiency may still be low (Birgersson and Ekvall, 1997; Fisher et al., 2002). Furthermore, the ability of infants to direct resources to various expenditures may depend on the composition (protein, lipid, carbohydrate) of the maternally provided nutrition and its rate of delivery (McAdam and Millar, 1999; Owens et al., 1993; Price and White, 1985). Therefore, as mortality in mammals is generally highest during the post-weaning stage (Clutton-Brock et al., 1987; Coulson et al., 2001; Le Boeuf et al., 1994; Van Ballenberghe and Mech, 1975), knowledge of infant growth strategies and how they differ according to environmental and maternal constraints may provide important insights into mechanisms influencing juvenile survival and life history.

Otariid seals (fur seals and sea lions) are an ideal group for investigating this topic, as females give birth to a single offspring, there is no post-weaning maternal care, and offspring are entirely dependent on milk for nutrition throughout most of lactation (Bonner, 1984). Furthermore, lactation in these species is characterised by mothers alternating between short nursing periods ashore and long foraging trips to sea during which their pup must fast (Gentry and Kooyman, 1986). Consequently, the nutritional resources delivered to the dependent pups must be allocated for growth, storage and behavioural development (e.g. learning to swim) during fasting periods as well as when the mother is ashore.

Lactation in otariid seals generally lasts 10–12 months, although in some species offspring may be suckled for up to 3 years (Bonner, 1984). Exceptions to this pattern are the Antarctic fur seal (*Arctocephalus gazella*) and the northern fur seal (*Callorhinus ursinus*), which have lactation periods lasting only 4 months. The brevity of lactation in these two species is thought to have evolved to exploit the predictably high but brief productivity of the subpolar summer and to maximise maternal transfer and offspring growth before the onset of the polar winter (Gentry and Kooyman, 1986). By contrast, the longer lactation periods of the other otariid species are thought to have evolved in response to the low seasonal variation but less predictable nature of the temperate and sub-tropical marine environments they inhabit. At three locations in the subantarctic region, however, there is the surprising situation where species representative of each strategy breed sympatrically. Macquarie Island, Marion Island and Iles Crozet are the northern and southern extents, respectively, of the Antarctic fur seal and subantarctic fur seal (*Arctocephalus tropicalis*) breeding ranges (Guinet et al., 1994; Kerley, 1984; Robinson et al., 2002). At these sites, the majority of pupping for each species occurs in December but, despite similarity in their maternal masses and pup birth masses (Goldsworthy et al., 1997; Kerley, 1985), Antarctic fur seal pups wean at the end of the Austral summer (March–April) whereas subantarctic fur seal pups wean in late winter (August–September). There are few examples worldwide of such closely related sympatric species having such divergent lactation strategies (Dempster et al., 1992; Innes and Millar, 1994).

Numerous studies have investigated the maternal characteristics (e.g. diet, foraging behaviour, foraging areas, colony attendance patterns and milk composition) and pup responses (e.g. growth rate and weaning mass) of Antarctic and subantarctic fur seals at their sympatric sites in order to understand the mechanisms driving the divergent strategies and their impacts (Goldsworthy, 1999; Goldsworthy and Crowley, 1999; Goldsworthy et al., 1997; Green et al., 1990; Kerley, 1983, 1984, 1985; Klages and Bester, 1998; Robinson et al., 2002). At Macquarie Island and Marion Island, no differences have been found in maternal diet, foraging areas or diving behaviour between the species during their summer lactational overlap (Goldsworthy and Crowley, 1999; Goldsworthy et al., 1997; Klages and Bester, 1998; Robinson et al., 2002) yet, over the same time period, growth rates of Antarctic fur seal pups are significantly greater than those of subantarctic fur seals at all sympatric sites (Goldsworthy and Crowley, 1999; Kerley, 1985; S. P. Luque et al., unpublished data). Goldsworthy and Crowley (1999) suggested that the difference in growth rates could reflect either a higher milk consumption rate in Antarctic fur seals or greater metabolic expenditure by subantarctic fur seals. However, the limited information on pup metabolic rates for the species is restricted to their allopatric sites (making comparisons difficult) and there is no information on their milk consumption rates at sympatric sites (Arnould et al., 1996a, 2001; Beauplet et al., 2003; Georges et al., 2001; Guinet et al., 1999). Furthermore, while mass gain differs between the species, it is not known whether the divergent lactation strategies influence the composition of growth and development (Owens et al., 1993; Spray and Widdowson, 1950).

The aims of this study, therefore, were to determine whether differences in body composition, metabolism and physiological development exist between sympatric Antarctic and subantarctic fur seal pups.

Materials and methods

Study site and animals

The study was conducted at La Mare aux Elephants (46°22′29″ S, 51°40′13″ E), Possession Island (Îles Crozet), during the 2001/2002 breeding season. Population growth rates for both Antarctic fur seals (*Arctocephalus gazella* Peters) and subantarctic fur seals (*Arctocephalus tropicalis* Gray) on Possession Island are currently ~18% per annum (Guinet et al., 1994). Annual pup productions at La Mare aux Elephants were 164 and 80 for Antarctic and subantarctic fur seals, respectively, in 2001/2002 and peak-pupping dates were 5 December and 25 December, respectively.

During the pupping period, 95 Antarctic and 58 subantarctic fur seal newborn pups were sexed and identified by a unique numbered piece of plastic tape glued to the fur on the top of the head (Georges and Guinet, 2000a). At about one month of age, each of these pups was tagged in the trailing-edge of both fore-flippers with an individually numbered plastic tag (Dalton Rototag, Nettlebed, UK). As part of concurrent studies, the attendance patterns of mothers of marked pups were monitored from birth until the end of March by visual inspection of the natal colony three times per day (09:00 h, 12:00 h and 17:00 h local time).

Sampling was conducted in February 2002 and was staggered by 10–15 days between the species in order to cover similar pup ages. Mean ambient and sea surface temperature during sampling were 8.0°C and 8.0°C, respectively (http//ingrid.ldgo.columbia.edu/). For all aspects of the study, selected pups were captured 1–3 days after the mother's departure to sea following a normal suckling period in order to allow sufficient time for complete voiding of ingested milk from the stomach (Arnould et al., 1996a; Donohue et al., 2002; Oftedal and Iverson, 1987). Each study pup was selected at random from the population of marked individuals and sampled for only one aspect of the study. Upon each capture, pups were weighed in a sack with an electronic suspension balance (±0.01 kg). All the study pups still had the black natal pelage and, based on close examination of the pelage, all individuals were considered to be at the pre-moult stage.

Respirometry and resting metabolic rate

Oxygen consumption, determined by an open circuit respirometry system (Butler and Woakes, 1982), was used to measure the resting metabolic rates (RMR) of pups. Pups were placed in a wooden respirometry chamber (80 cm×60 cm×50 cm; sealed with silicone and varnish) that was equipped with a small Plexiglas window and large fan that ensured complete and rapid mixing of air. Foam rubber seals ensured an air-tight junction between the door and the body of the respirometer. The chamber had a removable floor below which there was a basin 60 cm deep. The basin was filled with fresh water to within 10 cm of the rim and covered by a sheet of wire grating when a pup was placed in it.

Air was drawn through the respirometer using an air pump (B105; Charles Austen Pumps, Byfleet, Surrey, UK), and flow rate (maintained at 50 l min^{-1}) was measured using a rotameter (Fisher-Rosemount Ltd, Catham, Kent, UK). A subsample of the outlet air flow was passed through Drierite ($CaSO_4$) and CO_2 absorbent (Baralyme®) to an O_2 analyser (S103; Qubit Systems Inc., Kingston, Ontario, Canada). Sampling of ambient air was conducted every 10 min by manually switching a valve in the chamber outlet airflow line. The O_2 analyser was calibrated prior to each measurement period with atmospheric air and nitrogen (Air Products PLC, Crewe, Cheshire, UK). Ambient atmospheric pressure, temperature and humidity were measured on a digital barometer (Model BA116; Oregon Scientific Pty Ltd, Sydney, NSW, Australia) and recorded every 10 min. A humidity/temperature sensor was affixed inside the chamber.

The output signals from the O_2 analyser and the humidity/temperature sensor passed through a purpose-built interface box that amplified the signals to a range of –10 V to +10 V and then transferred them to an analogue–digital converter unit (DAQPad-1200; National Instruments Corporation, Austin, TX, USA) in a desktop computer. The computer sampled the outputs 100 times per second, took a mean of these values and saved them to a file every 1 s with a program developed using a software package for automatic instrumentation (LabView® 4.0; National Instruments Corporation). Ambient atmospheric pressure, temperature and humidity readings were manually entered into the software package as they were recorded. Water temperature was measured with a glass thermometer (±0.1°C; Hanna Instruments Ltd Pty, Keysborough, VIC, Australia) prior to, and immediately after, the pup was in the basin. For logistical reasons, the body temperature of study pups was not recorded.

The pups were introduced into the chamber and left to rest and acclimatise for 1 h. Measurements of O_2, humidity, temperature, pressure and flow were taken continuously throughout the duration of the experiment but for calculations of resting rates the values from the 10 min of minimum oxygen consumption after the hour of acclimatisation were used. Confirmation that the pup was resting but not sleeping was made by visual inspection through the Plexiglas window, which was usually kept covered. Once the measurements in air had been completed, the pup was placed in the water-filled basin and left to acclimatise for 1 h, and, thereafter, values from the 10 min of minimum oxygen consumption were used to calculate in-water standard rates. Due to equipment problems, in-air and in-water metabolic rates were not measured for all pups.

Oxygen consumption ($\dot{V}_{O_2}$) was calculated using the equation of Withers (1977):

$$\dot{V}_{O_2} = \frac{\dot{V}_{STPD} \times (F_{O_2,Amb} - F_{O_2,Exp})}{1 - F_{O_2,Amb} + RQ \times (F_{O_2,Amb} - F_{O_2,Exp})}\,, \qquad (1)$$

where $\dot{V}_{STPD}$ is the flow rate of dry air through the respirometer (in ml min^{-1}) corrected for standard temperature and pressure, $F_{O_2,Exp}$ and $F_{O_2,Amb}$ are the fractional concentrations of O_2 in outlet and ambient air, respectively, and RQ is the respiratory quotient. Assuming a diet of milk, an RQ of 0.71 was calculated with the following metabolic constants: 2.109 l O_2 g^{-1} lipid, 0.976 l O_2 g^{-1} protein, 1.433 l CO_2 g^{-1} lipid and 0.783 l CO_2 g^{-1} protein (Costa, 1987).

Body composition, daily energy expenditure and milk consumption

The body composition and daily energy expenditure (DEE) rates of pups were measured using hydrogen isotope dilution and doubly labelled water (DLW) techniques (Costa, 1987). After weighing upon capture, a background blood sample (5 ml) was collected into a heparinised syringe from each pup by venipuncture of an inter-digital vein in a hind-flipper. They were then given an intramuscular injection of a weighed dose (±0.01 g) of tritiated water (HTO; ~1 ml, 7.4 mBq ml^{-1}). Each animal was also given an oral dose, by stomach tube, of 15–20 ml $H_2{}^{18}O$ 10% AP (Isotec Inc., Miamisburg, OH, USA). Pups were then kept in an enclosure for 3 h before an equilibration blood sample (5 ml) was collected, to determine the total body water (TBW) pool size and initial plasma ^{18}O levels, before being released at the point of capture, left undisturbed and allowed to suckle normally during the next visit ashore by their mother. Each pup was recaptured 2–3 days after the departure of the mother on her subsequent foraging trip to sea (4–6 days after initial capture), weighed and a final blood sample (5 ml) was collected.

All blood samples were kept at 4°C for several hours before being centrifuged (3000 r.p.m., for 10 min) and the plasma fraction separated. Aliquot samples (2–5 ml) of plasma were stored frozen (–20°C) in plastic screw-cap vials (with silicon O-rings; Sarstedt Inc., Newton, NC, USA) until analysis. For tritium analysis, thawed sub-sample aliquots of plasma (0.2 ml) were distilled into pre-weighed scintillation vials following the procedures of Ortiz et al. (1978). The vials were then re-weighed to obtain the mass of the sample water (±0.1 mg). Scintillant (10 ml Ultima Gold; Canberra Packard, Mt Waverly, VIC, Australia) was added to the vials, which were then counted for 5 min in a Packard Tri-Carb 2100TR liquid scintillation analyser (Canberra Packard) with correction for quenching by means of the sample channels ratio and an external standard to set the counting window for each vial. Samples were analysed in duplicate and each vial was counted twice. Sub-samples (0.2 ml) of the injectant were counted in the same way, and at the same time, as the water from the plasma samples to determine the specific activity of the tritium injected. The ^{18}O enrichment of plasma water was determined by Metabolic Solutions (Nashua, NH, USA) using gas isotope ratio mass spectrometry.

TBW was calculated from HTO dilution space using an equation determined empirically in Antarctic fur seal pups (Arnould et al., 1996b). Lean body mass (LBM) was calculated from TBW assuming a hydration constant of 74.7% (Arnould et al., 1996b), and total body lipid (TBL) was calculated by subtracting LBM from total body mass. Total water influx (TWI) rates were calculated from the decrease in specific activity of HTO and equations 5 and 6 in Nagy and Costa (1980), assuming an exponentially changing TBW. Carbon dioxide production rates were calculated using equation 3 of Nagy (1980). DEE was calculated from CO_2 production assuming a conversion factor of 27.44 $kJ\ l^{-1}\ CO_2$ (Costa, 1987). Oxygen consumption was determined by dividing CO_2 production by the RQ (0.71; see above). Metabolic water production (MWP) rates were calculated from the metabolic rate determined by DLW assuming a conversion factor of 0.02629 $g\ H_2O\ kJ^{-1}$ (Schmidt-Nielsen, 1983).

Milk consumption rates were calculated using the following equation (Ortiz, 1987):

$$\text{Milk consumption rate} = \frac{\text{TWI} - \text{MWP}}{\text{Milk water content}}\ . \qquad (2)$$

Milk composition does not differ significantly between Antarctic and subantarctic fur seals at the study site, and mean milk water and energy contents during the study period were 41.5% and 18.9 $kJ\ g^{-1}$, respectively (S. P. Luque et al., unpublished data). Similar findings have been reported on Macquarie Island (Goldsworthy and Crowley, 1999).

Blood volume

The physiological ability of infant pinnipeds to make foraging dives has been shown to increase throughout the period of maternal dependence (Burns, 1999; Horning and Trillmich, 1997a,b). In the present study, therefore, factors affecting oxygen storage [haematocrit (Hct), haemoglobin (Hb) and total blood volume] were measured and used as indices of physiological development.

After weighing upon capture, a background blood sample (5 ml) was collected into a heparinised syringe from each pup by venipuncture of an inter-digital vein in a hind-flipper and stored cool (4°C) until all samples were centrifuged (see below). Each pup was then given an intravenous injection (~1 ml) of a weighed dose of Evans Blue dye (0.5 $mg\ kg^{-1}$ body mass; Sigma-Aldrich, St Louis, MO, USA) to measure total blood volume (El-Sayed et al., 1995). After completing the injection but before removing the needle from the blood vessel, the syringe was flushed with blood 2–3 times to ensure that all dye was administered. Serial blood samples (5 ml) were collected at 10 min, 20 min and 30 min post-injection to measure the equilibration and dilution of the dye (El-Sayed et al., 1995).

Prior to centrifugation, each background blood sample was thoroughly mixed by gentle agitation. An 20 μl sample was placed in 2.5 ml of Drabkins reagent (Sigma kit 525A; Sigma-Aldrich) and later assayed for Hb concentration by colorimetric analysis. Absorbance was measured in duplicate samples on a Spectronic 1001 (Milton Roy, Ivyland, PA, USA) spectrophotometer at a wavelength of 540 nm. Hb concentration of each sample was determined by comparison with a dilution curve created from protein standards. Hct was measured in triplicate from an aliquot of the whole blood as the packed red blood cell volume in capillary tubes following centrifugation for 5 min at 11 500 r.p.m.

Total blood volume was measured by colorimetric analysis of the Evans Blue dilution. Following centrifugation at 3000 r.p.m. for 10 min, aliquots of plasma were separated and stored frozen (–20°C) in plastic vials until analysis several months later. In the laboratory, the thawed samples were agitated and centrifuged again at 3000 r.p.m. for 5 min. The absorbance of the decanted dyed plasma was determined on a Spectronic 1001 (Milton Roy) spectrophotometer at 624 nm and 740 nm following procedures outlined in Foldager and Blomqvist (1991). Dye concentrations were determined from a serial dilution curve of Evans Blue standards measured at both wavelengths. It is common practice to back-calculate the dye concentration at the time of injection by determining the intercept of a regression line between dye concentration of each serial sample and the time it was collected (Costa et al., 1998; El-Sayed et al., 1995; Foldager and Blomqvist, 1991). This method was not used because the regression between dye concentration and time post-injection for most of the seals was not statistically significant ($P>0.05$). Therefore, a mean dye concentration using all three samples (i.e. 10 min, 20 min and 30 min post-injection) was calculated and used for determination of blood volume. Plasma volume was calculated as follows:

$$V_\mathrm{p} = \frac{[m_\mathrm{i}]}{[C_\mathrm{e}]}\ , \qquad (3)$$

where [m_i] is the initial quantity (mg) of Evans Blue dye injected, [C_e] is the concentration of Evans Blue dye (mg l^{-1}) obtained from the mean of the serial samples and V_p is plasma volume (litres). Total blood volume (V_b) was then calculated as:

$$V_b = V_p\,[100\,(1 - \mathrm{Hct})] - 1\,, \tag{4}$$

where Hct is haematocrit expressed as a fraction of whole blood.

Statistical analyses were performed using the Systat® statistical software (Version 7.0.1; SPSS Inc., Richmond, CA, USA). The Kolmogorov–Smirnov test was used to determine whether the data were normally distributed, and an F test was used to confirm homogeneity of variances ($P>0.2$ in all cases). Differences between linear regressions were tested by analysis of covariance (ANCOVA) after testing for homogeneity of slopes. Unless otherwise stated, data are presented as means ± 1 S.E.M. and results considered significant at the $P<0.05$ level.

Results

Resting metabolic rate

Measurements of in-air resting metabolic rate (RMR) were obtained for 14 Antarctic (six female, eight male) and 14 subantarctic (seven female, seven male) fur seal pups. Mean ambient air temperature during measurements was 10.5±0.6°C (range: 6–15°C). In-air RMR of pups was significantly positively related to body mass in Antarctic fur seals ($r^2=0.58$, $P<0.02$) but not subantarctic fur seals ($P>0.2$; Fig. 1). Mass-specific in-air RMR did not differ significantly between the sexes in either species ($P>0.1$ in both cases) so the data were combined (Table 1). Mean mass-specific in-air RMR of pups was significantly greater in Antarctic fur seals (17.1±0.6 ml O_2 kg^{-1} min^{-1}) than subantarctic fur seals (14.1±0.5 ml O_2 kg^{-1} min^{-1}; $t_{26}=3.82$, $P<0.001$).

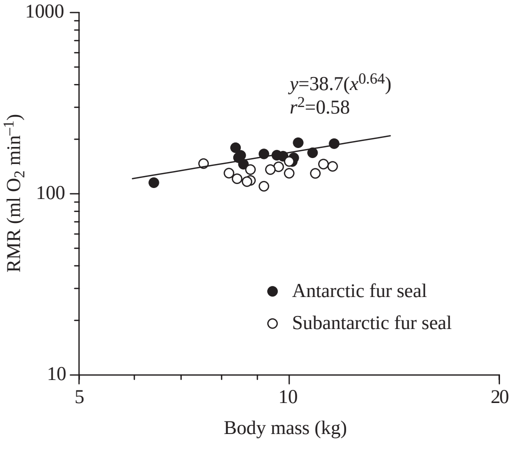

Fig. 1. The relationship between in-air resting metabolic rate (RMR) and body mass of Antarctic and subantarctic fur seal pups at Possession Island, Îles Crozet. The equation given is for Antarctic fur seal pups. No significant relationship was found for subantarctic fur seals.

Measurements of in-water standard metabolic rate (SMR) were obtained for 12 Antarctic (six female, six male) and 15 subantarctic (seven female, eight male) fur seal pups. Mean water temperature during the measurements was 10.0±0.6°C (range: 9–12°C). There was no relationship between body mass and in-water SMR in either species ($P>0.1$ in both cases). Mass-specific in-water SMR did not differ significantly between the sexes in either species ($P>0.1$ in both cases) so the data were combined (Table 1). Mean mass-specific in-water SMR of pups was significantly greater in Antarctic (22.9±2.5 ml O_2 kg^{-1} min^{-1}) than subantarctic fur seals (14.6±1.0 ml O_2 kg^{-1} min^{-1}; $t_{25}=3.41$, $P<0.003$).

Measurements of both in-air RMR and in-water SMR were made in 10 Antarctic and 13 subantarctic fur seal pups. Mean in-water SMR was significantly greater than in-air RMR for Antarctic fur seal pups (paired t-test, $t_9=2.59$, $P<0.03$) but not for subantarctic fur seal pups ($t_{12}=0.82$, $P>0.4$).

Body composition, daily energy expenditure and milk consumption

Body composition upon capture was determined for a total of 16 (eight male, eight female) Antarctic and 14 subantarctic (seven male, seven females) fur seal pups. No significant differences were detected between the sexes in either species ($P>0.2$ in both cases) so the data were combined. As expected, significant positive correlations were found between total body water (TBW) and body mass in both species (Fig. 2). However, the regressions differed significantly between the species (ANCOVA, $F_{1,27}=5.82$, $P<0.02$), with Antarctic fur seal pups having higher TBW per unit mass and, thus, relatively lower TBL stores (22.2±1.0%) than subantarctic fur seal pups (26.1±1.0%; $t_{28}=2.73$, $P<0.02$; Table 2).

With the exception of one female Antarctic fur seal pup (^{18}O levels were too close to background upon recapture), field metabolic rate measurements were obtained for all of the above individuals. There were no significant differences in CO_2 production between the sexes for either species ($P>0.1$ in both cases) so data were combined. Antarctic fur seal pups

Table 1. *Mass-specific metabolic rates of Antarctic and subantarctic fur seal pups on Possession Island, Îles Crozet*

	Antarctic fur seal	N	Subantarctic fur seal	N
Body mass (kg)	9.64±0.43	14	9.45±0.31	15
Age (days)	64±1	14	62±1	15
In-air RMR (ml O_2 kg^{-1} min^{-1})	17.1±0.6*	14	14.1±0.5*	14
In-water SMR (ml O_2 kg^{-1} min^{-1})	22.9±2.5†	12	14.6±1.0†	15

Values are means ± S.E.M.

* and † denote significant differences at $P<0.001$ and $P<0.003$, respectively.

RMR, resting metabolic rate; SMR, standard metabolic rate.

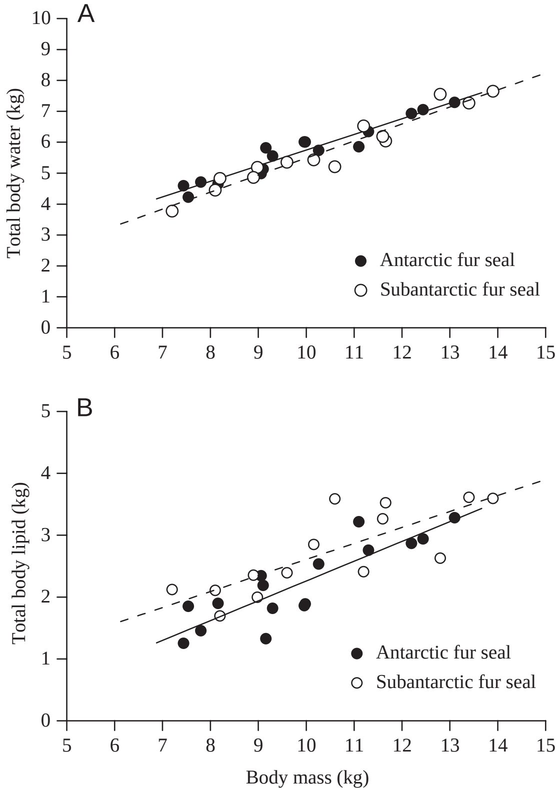

Fig. 2. The relationship between body mass and (A) total body water and (B) total body lipid in Antarctic (solid lines) and subantarctic (broken lines) fur seal pups at Possession Island, Iles Crozet. Regression statistics for both species in A: y=0.50x+0.70 (r^2=0.93, P<0.0001) and y=0.55x–0.01 (r^2=0.93, P<0.0001), respectively. Regression statistics for both species in B: y=0.32x–0.94 (r^2=0.75, P<0.0001) and y=0.26x+0.02 (r^2=0.63, P<0.0001), respectively.

Table 2. *Energy expenditure and milk consumption rates of Antarctic and subantarctic fur seal pups on Possession Island, Îles Crozet*

	Antarctic fur seal (N=15)	Subantarctic fur seal (N=14)
Body mass (kg)	10.05±0.35	10.47±0.49
Age (days)	64±1	66±2
Total body lipid (%)	22.2±1.0†,‡	26.1±1.0†
CO_2 production (ml g^{-1} h^{-1})	0.97±0.05*	0.81±0.05*
Daily energy expenditure (kJ kg^{-1} day^{-1})	638±33*	533±33*
O_2 consumption (ml g^{-1} h^{-1})	1.36±0.07*	1.14±0.07*
Total water influx (ml kg^{-1} day^{-1})	51.2±2.7†	40.7±3.5†
Metabolic water production (ml kg^{-1} day^{-1})	16.8±0.8*	14.0±0.9*
Milk water intake (ml kg^{-1} day^{-1})	34.4±3.0	26.2±3.9
Milk consumption (ml kg^{-1} day^{-1})	82.9±7.1	63.2±9.5
Milk consumption (ml bout^{-1})	3879±260	3637±544

* and † denote significant differences between the species at P<0.03 and P<0.02, respectively. ‡n=16 (see text for details).

had a significantly higher mean CO_2 production rate (0.97±0.05 ml g^{-1} h^{-1}) than subantarctic fur seal pups (0.81±0.05 ml g^{-1} h^{-1}; t_{27}=2.36, P<0.03). These values represent mean daily energy expenditure (DEE) and O_2 consumption rates, respectively, of 638±33 kJ kg^{-1} day^{-1} and 1.36±0.07 ml g^{-1} h^{-1} for Antarctic fur seals and 533±33 kJ kg^{-1} day^{-1} and 1.14±0.07 ml g^{-1} h^{-1} for subantarctic fur seal pups (Table 2). The higher DEE of Antarctic fur seal pups resulted in them having significantly greater metabolic water production (MWP) rates (16.8±0.8 ml kg^{-1} day^{-1}) than subantarctic fur seal pups (14.0±0.9 ml kg^{-1} day^{-1}; t_{27}=2.36, P<0.03). Mean milk water intake (MWI), however, did not differ significantly between the species (t_{27}=1.66, P>0.1; Table 2). Consequently, as milk composition did not differ between the species (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data), there was no significant difference between the species in the amount of milk consumed per day by pups during the study period (t_{27}=1.70, P>0.1; Table 2). The amount of milk consumed per maternal attendance bout also did not differ significantly between the species (t_{27}=1.70, P>0.1).

Blood volume

Haematocrit (Hct) and haemoglobin (Hb) values were obtained for 10 (five male, five female) Antarctic and eight subantarctic (five male, three female) fur seal pups. There were no significant differences in either Hct or Hb between the sexes for either species (P>0.1 in all cases) so data were combined. Mean Hct did not differ significantly between Antarctic (50.2±0.9%) and subantarctic (48.1±1.0%) fur seal pups (t_{16}=1.5, P>0.1). Similarly, there was no significant difference in Hb content between Antarctic (14.5±0.3 g dl^{-1}) and subantarctic (14.6±0.4 g dl^{-1}) fur seal pups (t_{16}=0.25, P>0.8).

Blood volume estimates were obtained for five Antarctic (two male, three female) and six subantarctic (four male, two female) fur seal pups. Blood volume as a proportion of body mass was significantly greater in Antarctic (11.5±0.8%) than subantarctic (8.9±0.5%) fur seal pups (t_9=2.81, P<0.03). Assuming the same mean body composition for these pups as determined above, the difference in blood volume between the species was still significant when considered as a proportion of LBM (t_9=2.35, P<0.05).

Discussion

Body composition, resting metabolic rate and daily energy expenditure

In contrast to numerous recent studies that have documented higher mass-specific body lipid contents in female than male fur seal pups (Arnould et al., 1996a, 2001; Arnould and

Hindell, 2002; Beauplet et al., 2003; Donohue et al., 2002), no significant differences in body composition were observed between the sexes of either species in the present study. However, as with the lack of sex differences in other variables measured in the present study (e.g. mass-specific in-air RMR and in-water SMR), this is likely to be due to low statistical power because, with the small sample sizes used, only differences of >30% would have been detected (at an alpha of 0.05 and a power of 0.9). The TBL of Antarctic fur seal pups observed in the present study (22%) is within the range previously recorded for conspecific pups at South Georgia and Iles Kerguelen (Arnould et al., 1996a, 2001; Lea et al., 2002). By contrast, the TBL of subantarctic fur seal pups (26%) is substantially greater than that recorded for conspecific pups of approximately the same age at Amsterdam Island (8–12%; Beauplet et al., 2003). This difference may reflect a reduced need for subcutaneous blubber insulation in the warmer temperate climate of Amsterdam Island. Interestingly, despite similar maternal foraging trip durations during the present study (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data), subantarctic fur seal pups had significantly greater TBL than Antarctic fur seal pups. These data are consistent with those collected from a larger sample size (*N*=41 and 47, respectively, for the two species) throughout the summer overlap in lactation (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data).

The in-water SMR of Antarctic fur seal pups was significantly greater than their in-air RMR. Similar findings have been reported in comparable ambient and water temperatures for similar-aged pre-moult northern fur seals (Donohue et al., 2000). The ratio of in-water SMR to in-air mass-specific RMR, however, was substantially lower in Antarctic fur seals (1.3) than in northern fur seals (2.4), due primarily to the greater in-water mass-specific SMR (37 ml O_2 kg^{-1} min^{-1}) yet similar RMR (15 ml O_2 kg^{-1} min^{-1}) of the latter species. Baker and Donohue (2000) found that pre-moult northern fur seal pups spent little time in water, and Donohue et al. (2000, 2002) suggested that this was due to their inability to thermoregulate efficiently in water at that age. By contrast, Antarctic fur seal pups in the present study spent considerable amounts of time swimming in shallow water close to the shore (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data), and similar-aged pups on South Georgia have been recorded as spending up to 50% of their time in the water (McCafferty et al., 1998). It is possible, therefore, that pre-moult Antarctic fur seals are better able to thermoregulate in water than northern fur seal pups. Indeed, the higher body lipid content (22%) of Antarctic fur seal pups in the present study compared with that of northern fur seal pups (15%; Donohue et al., 2000) is likely to provide them with greater subcutaneous thermal insulation.

Unexpectedly, in contrast to Antarctic fur seal pups, in-water SMR of subantarctic fur seal pups was not significantly greater than their in-air RMR. This could indicate that pre-moult subantarctic fur seal pups have better thermoregulatory capabilities than Antarctic fur seal pups. If this was the case, pre-moult subantarctic fur seal pups might be expected to spend considerable amounts of time in water developing important swimming and diving skills (Baker and Donohue, 2000; McCafferty et al., 1998). However, while the 4% greater body lipid content of subantarctic fur seal pups might provide them with some advantage in thermal insulation, they were rarely seen in water during the study (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data, see below), suggesting that they do not have exceptional thermoregulatory capabilities. An alternative explanation is that pre-moult pups of this species have less developed thermoregulatory ability than Antarctic fur seal pups, and immersion in water, representing a severe thermal challenge they would not normally experience, resulted in metabolic depression (Boily and Lavigne, 1996; Lee et al., 1997). Unfortunately, core body temperature could not be measured in the present study, so this proposition cannot be investigated. Additional studies determining the thermal conductance of subantarctic fur seal pups both in water and in air are required to elucidate the reasons behind the unexpected findings of their similar in-air RMR and in-water SMR.

A further surprising finding of the present study was that Antarctic fur seal pups had a mean in-air mass-specific RMR 21% higher than that of subantarctic fur seal pups. The higher TBL of subantarctic fur seals may have provided them with some thermoregulatory advantage and, conversely, the corresponding higher LBM of Antarctic fur seals would result in a greater metabolically active mass and, thus, higher metabolic costs. On their own, however, these factors are unlikely to account for the large differences in RMR. One possibility is that the higher RMR of Antarctic fur seal pups is related to their generally greater levels of activity (see below). Numerous studies with humans and rats have shown that sustained increases in daily activity levels result in the elevation of RMR (Byrne and Wilmore, 2001; Poehlman and Danforth, 1991; Tremblay et al., 1992).

Concomitant with a higher mass-specific RMR, Antarctic fur seal pups also had a daily energy expenditure 20% greater than that of subantarctic fur seal pups. This is consistent with opportunistic observations at the study site of subantarctic fur seal pups spending significantly less time in both terrestrial and aquatic activities than Antarctic fur seal pups, preferring instead to sleep (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). Indeed, the low DEE recorded for subantarctic fur seal pups at Amsterdam Island (see below) has been attributed to their low activity levels (Beauplet et al., 2003). The ratio of DEE to in-air RMR was 1.3 for both species, which is less than the ratio of 1.7 reported for pre-moult Antarctic fur seal pups at South Georgia and northern fur seal pups (Arnould et al., 2001; Donohue et al., 2002). The DEE of Antarctic fur seal pups in the present study (638 kJ kg^{-1} day^{-1}) is less than the DEE reported for free-ranging pre-moult northern fur seal pups (700 kJ kg^{-1} day^{-1}; Donohue et al., 2002) and conspecific pups of similar age on South Georgia (1044 kg^{-1} day^{-1}; calculated from MWP values in Arnould et al., 2001). These differences may reflect the colder ambient and sea water temperatures during summer at the Pribilof Islands (5°C and 4°C, respectively; http://ingrid.ldeo.columbia.edu/SOURCES/.IGOSS/) and South Georgia (4°C and 3°C, respectively; British Antarctic Survey, unpublished data) in comparison with those during the present study (8°C and 8°C, respectively; http://ingrid.ldeo.columbia.edu/SOURCES/.IGOSS/), leading to higher thermoregulatory costs. Similarly, the difference between the DEEs of pre-moult subantarctic fur seal pups in the present study (533 kJ kg^{-1} day^{-1}) and on Amsterdam Island (416 kJ kg^{-1} day^{-1}; Beauplet et al., 2003) may reflect the substantially warmer summer climate of the latter (17°C and 18°C for ambient and sea water temperatures, respectively; Meteo France, unpublished data).

Errors in calculating DEE from CO_2 production values can arise if incorrect RQ values are assumed (Costa, 1988; Nagy, 1980). Indeed, differences in body composition may reflect differences in metabolic fuel use (Beauplet et al., 2003; Blaxter, 1989) such that differences in calculated DEE could be an artefact of RQ assumptions. In the present study, however, if subantarctic fur seal pups were catabolising proportionately more protein than were Antarctic fur seal pups (as might be suggested by their body composition differences) then the difference in DEE between the species would actually be greater.

Milk consumption and growth strategy

The lack of any significant difference in daily or per bout milk consumption between Antarctic and subantarctic fur seal pups is consistent with the similarity in foraging trip durations of their mothers (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). The mean daily milk energy consumption by Antarctic fur seal pups in the present study (1.6 MJ kg^{-1} day^{-1}) is the same as that recorded for pre-moult conspecific pups at South Georgia (1.6 MJ kg^{-1} day^{-1}; Arnould et al., 1996a) and similar to that reported for pre-moult northern fur seal pups (1.4 MJ kg^{-1} day^{-1}; Donohue et al., 2002). By contrast, consumption by subantarctic fur seal pups (1.2 MJ kg^{-1} day^{-1}) is greater than reported for similar-aged pre-moult pups of the Australian fur seal (*A. pusillus doriferus* Jones; 0.8 MJ kg^{-1} day^{-1}), a temperate species with a comparable lactation length (Arnould and Hindell, 2002). Unfortunately, milk consumption estimates are not available for other fur seal species or for subantarctic fur seals at allopatric colonies, so it cannot be ascertained whether pups of this nominally temperate species normally consume such quantities of milk or if this only occurs at the subantarctic breeding sites. Comparison of subantarctic fur seal pup growth rates during the first four months at sympatric colonies (e.g. present study site, 70 g day^{-1}, S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data; Marion Island, 72 g day^{-1}, Kerley, 1985) with those at allopatric colonies further north (Gough Island, 58 g day^{-1}, Kirkman et al., 2002; Amsterdam Island, 54 g day^{-1}, Guinet and Georges, 2000), however, would tend to suggest a greater milk consumption by pups at the subantarctic sites during this period.

As has been reported on Marion and Macquarie islands (Goldsworthy and Crowley, 1999; Kerley, 1985), Antarctic fur seal pup growth rates are significantly greater than those of subantarctic fur seals at the present study site on Possession Island (80 g day^{-1} and 70 g day^{-1}, respectively; S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). This finding appears inconsistent with the observed parity in milk consumption, especially in conjunction with the observed differences in the rates of energy expenditure. Differences in body composition, however, could account for this apparent contradiction. As adipose tissue is more energy dense than lean mass, its deposition requires greater amounts of nutrition (Blaxter, 1989). This is especially so in infant mammals, where the hydration of lean body mass is 3–4% greater than in physiologically mature adults (Adolph and Heggeness, 1971; Arnould et al., 1996b; Reilly and Fedak, 1990). Furthermore, if the observed body composition differences reflect differences in metabolic substrate use, as has recently been shown for sex-based body composition differences in subantarctic fur seals at Amsterdam Island (Beauplet et al., 2003), preferential lipid catabolism could provide Antarctic fur seals with the additional energy to account for their greater metabolic expenditure. Consequently, it is feasible that equal milk energy consumption could produce the differing growth rates.

A question that the findings of this study pose is why do Antarctic fur seal pups not conserve energy and accumulate greater lipid reserves to sustain them once they are weaned, especially as food availability may be reduced during the colder winter months? Why do they have higher energy expenditure rates than their sympatric congenerics? Pups of this species only have four months in which to develop all the swimming and diving skills necessary to forage independently (Bonner, 1984). While greater lipid reserves would provide some advantages (e.g. thermal insulation, 'nutritional buffer'), their benefit would be limited if pups did not have any ability to dive and know how to hunt at weaning. Hence, selection should favour the early acquisition of necessary behavioural skills relative to species with longer maternal dependence. Comparison of the diving behaviour of Antarctic and subantarctic fur seal pups at Possession Island indicates that the former do indeed spend greater amounts of time in water and learning to dive at an earlier age (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). Such increased activity would lead to a higher energy expenditure (Baker and Donohue, 2000; Donohue, 1998). Consistent with this earlier development of diving behaviour in Antarctic fur seals is the finding of the present study that pups of this species have greater mass-specific blood volumes than do subantarctic fur seal pups. As Hb and Hct content did not vary between the species, the larger blood volume translates into greater blood oxygen stores in Antarctic fur seal pups (El-Sayed et al., 1995). Blood oxygen storage capacity in pinnipeds generally increases with age until maturity (Costa et al., 1998; Horning and Trillmich, 1997a; Jorgensen et al., 2001). Consequently, the results of the present study suggest that physiological development is faster in Antarctic than in subantarctic fur seal pups.

The converse question posed by the findings of the present study is, as pups of both species appear to receive similar amounts of nutrition during the summer overlap in lactation, why do subantarctic fur seal pups not devote more resources to faster behavioural and physiological development? The answer may lie in the 'anticipation' of a reduced rate of nutrient delivery during the winter months. While there is no corresponding information available for the present study site on Possession Island, average winter maternal foraging trips of subantarctic fur seals at both Amsterdam Island and Marion Island are the longest recorded for any otariid species (23–28 days; Georges and Guinet, 2000b; Kirkman et al., 2002). The fasting durations experienced in winter by pups at these sites, therefore, are some of the most extreme for any infant mammal (Guinet and Georges, 2000). Pups endure these fasts by greatly reducing activity, adopting protein conserving pathways and relying mainly on lipid catabolism for metabolic energy (Beauplet et al., 2003). Furthermore, initial body lipid stores and daily mass loss in these pups are, respectively, positively and negatively related to the fasting durations endured (G. Beauplet, unpublished data; Guinet and Georges, 2000). Hence, a strategy of limiting energy expenditure and directing nutritional resources to adipose tissue growth by subantarctic fur seal pups during the summer months may be an adaptation for accumulating sufficient lipid reserves to survive repeated extreme fasts later in lactation.

In summary, the results of the present study indicate that differences exist in the resting metabolic rates, total energy expenditure and development between Antarctic and subantarctic fur seal pups, two closely related congeneric species (Wynen et al., 2001), at a sympatric breeding site. These differences are consistent with adaptations for rapid development of foraging abilities necessary for the earlier nutritional independence in the former and extended periods of fasting during prolonged maternal dependence in the latter. The mechanisms controlling the physiological differences observed between the two species are unknown but are likely to involve thyroid hormones, which are known to play an important role in regulating metabolism and development in neonatal mammals (Bernal and Refetoff, 1977). While thyroid hormones have been shown to vary throughout development, lactation and between seasons in phocid seals (Haulena et al., 1998; John et al., 1987; Little, 1991; Litz et al., 2001; Ortiz et al., 2001; Woldstad and Jenssen, 1999), their dynamics in otariid seals remain to be investigated.

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