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ORIGINAL PAPER

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Seasonal use of oceanographic and fisheries management zones by juvenile southern elephant seals (*Mirounga leonina*) from Macquarie Island

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Abstract The foraging distribution of marine predator populations is important for effective modelling and management of pelagic marine systems. We tracked 31 juvenile southern elephant seals from Macquarie Island (158°57′E, 54°30′S) over their annual post-moult and mid-year trips to sea. We calculated the amount of time spent in regional fisheries management areas and within bounded oceanographic regions. During the austral summer, juvenile seals spent over 90% of their time south of the Antarctic Polar Front and ~80% within fisheries management regions [Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and exclusive economic zones]. In winter, seals spent ~75% of their time in the region bounded by the Antarctic Polar Front and the southern boundary of the Antarctic Circumpolar Current, and ~60% within fisheries management regions. The time spent per region differed significantly between summer and winter. Our results demonstrate that juvenile southern elephant seals from Macquarie Island spent more time south of the Antarctic Polar Front and within fisheries management areas than previously suspected.

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Introduction

The Southern Ocean is a dynamic, highly variable environment with an unpredictable and patchy distribution of biological resources (El-Sayed 1988; Constable et al. 2003). The Southern Ocean has been the focus of many studies (Orsi et al. 1995; Rintoul et al. 1997; Budillon and Rintoul 2003) that have identified broad- and fine-scale structure according to the physical properties of the region's different water masses. These physical divisions provide a diversity of habitats that influence the distribution, diversity and abundance of the ecological communities (Lutjharms 1990; Rodhouse and White 1995; Arrigo et al. 1998; Constable et al. 2003).

Living resources in the Southern Ocean are managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) under Article IX of the Antarctic treaty system. The CCAMLR was designed to safeguard the marine environment, to protect the integrity of the ecosystem of the seas surrounding Antarctica and to allow the exploitation of resources within (Agnew 1997). As part of the management framework, the CCAMLR environmental monitoring program (CEMP) was initiated in 1985 to relate indices of predator status and breeding success to krill availability, and to distinguish these relationships from those resulting from harvesting or natural changes (Agnew 1997). The aim of the program was to focus on krill before overfishing could have serious consequences (Nicol 1991). However, this focused approach has meant that CCAMLR has devoted less attention to the open-ocean pelagic system. Although commercial fishing pressure has recently increased within this system, several regions have still had little fishing and present an opportunity to distinguish variation in biological and physical parameters (e.g., climate change—Viet et al. 1996; Barbraud and Weimerskirch 2001; Weimerskirch et al. 2003) from that due to harvesting.

Top predators have sometimes been proposed as indicators of the status of components of lower-trophic levels (Furness et al. 1993; Kerry et al. 1997; Croxall et al. 1999; Barbraud and Weimerskirch 2001). This approach has been adopted by CEMP in an attempt to understand and model the krill-based system (Agnew 1997; Croxall et al. 1999; Hindell et al. 2003a). In the open-ocean pelagic system, one possible indicator predator that is easily accessible and has a circumpolar distribution is the southern elephant seal (*Mirounga leonina*). This species is a wide-ranging, deep-diving predator that spends more than 80% of its annual cycle at sea. They are major consumers of second-order producers, primarily squid and fish (Bradshaw et al. 2003; Hindell et al. 2003b). Further, it has been suggested that this species is susceptible to changes in the availability of prey (Hindell et al. 1994; Guinet et al. 1999; Slip and Burton 1999; McMahon et al. 2003), which is reflected in the status of the different populations (McMahon 2003).

A recent demographic study has shown that the survival of juveniles (aged 1–4 years) is the most important factor influencing the rate of change of elephant seal populations (McMahon et al. 2003) at Macquarie Island. As they progress from juvenile to adult foraging patterns, juveniles may be influenced by ontogenetic changes in morphology, diving behaviour, foraging areas of the Southern Ocean, the availability of prey or a combination of these factors (Hindell et al. 1994) and, therefore, may be more sensitive than adults to variation in their environment.

Although there have been several studies of the foraging ecology of southern elephant seals from Macquarie Island (Slip et al. 1994; Hindell et al. 1991a, b, 1999, 2003b; Irvine et al. 2000; Field et al. 2001; van den Hoff et al. 2002; McConnell et al. 2002), most have concentrated on the adult population or naive, recently weaned pups. Only one study has described the at-sea movements of juvenile seals (van den Hoff et al. 2002), and this was limited to seals less than 18 months old. It is therefore important to examine the foraging ecology of juvenile seals, especially given that juveniles within the Macquarie Island population constitute almost half the total population (McMahon 2003).

In this study, we specifically aimed to (1) describe the regions of the Southern Ocean used by the different juvenile age-groups, (2) determine whether there were differences in areas or time spent within broad oceanographic regions of the Southern Ocean relative to the time of the year (summer vs winter), and (3) determine how much time the seals spent within fisheries management zones.

Materials and methods

Derivation of spatial and temporal data

The southern elephant seal population at Macquarie Island (158°57′E, 54°30′S) has been the focus of a long-term demographic study since 1993 (McMahon et al. 2003). Approximately 2,000 pups were marked each year (using plastic flipper tags and hot-iron branding; McMahon et al. 1997) from 1993 to 2000. For the present study, juvenile seals were regarded as those between 1 and 4 years old that had not bred before (McMahon 2003). The 3-year old sample was biassed towards females that were tracked only until their first breeding season and not over an entire annual cycle. One-year-old seals, from 12 to 24 months old, are referred to as ‘yearlings’, and after that as 2- and 3-year olds.

We used simple temperature–light loggers (LL; Platypus Engineering, Kingston, Tasmania, Australia) and temperature-time-depth recorders (TDRs; Wildlife Computers, Redmond, USA) to provide location data for the juvenile seals. The LL units were 60×45×25 mm and include an 8 megabit FLASH memory for storage of data. Light and temperature data were collected every 45 s. The temperature sensor had a resolution of ±0.2°C and a range of −12 to 31°C. The TDRs were Mk3–Mk7 models that measured temperature, depth (pressure) and light at the same sampling interval as the LLs.

Thirty-one juvenile seals were equipped with TDRs or LLs between 1999 and 2001 (3 in 1999/2000 and 28 in 2000/2001), encompassing 65 individual foraging trips. Over their annual cycle juvenile seals only have to return to land to moult (November–December) but they also return during the winter to haul-out, the reason for which is unclear (Hindell and Burton 1988; Kirkman et al. 2001; Wheatley 2001). Some seals may even return twice for this ‘winter’ or ‘mid-year’ haul-out. Seals were caught by hand as they were about to leave the island at the end of their annual moult using the technique of McMahon et al. (2000) and anaesthetized intravenously using prescribed doses of TELAZOL (Field et al. 2002). The LLs and TDRs were attached to the hair on the dorsal surface of the seals using two-part epoxy (Araldite 268, Ciba Geigy).

Estimation of location from light levels

At-sea locations were derived using geo-location software (Multi-trace, Jensen Software, Germany) that gave two locations per day (Bradshaw et al. 2002). Positions that would have exceeded the maximum distance that could have been travelled per unit time (12.5 km h^{-1} McConnell et al. 1992; Bradshaw et al. 2002) were excluded. During the equinox periods (4 March–14 April and 30 August–14 October) when latitudes could not be estimated due to the invariance of day length, we used linear interpolation to the next reliable latitude to provide an estimate of the daily latitude. Daily positions were then filtered using a state-space Kalman location filter (Sibert et al. 2003).

Spatial and temporal summary

Once the location data were filtered, they were rasterised (i.e., converted from point data into gridded data) onto a 300 km ×300 km grid using interactive data language (IDL 5.0-Research Systems, USA) routines. The size of the grid cells were set conservatively to allow for maximum distance that the seals could travel (between an average of 70–90 km day^{-1}; McConnell and Fedak 1996; Le Boeuf et al. 2000) and the errors associated with geo-location estimates (Bradshaw et al. 2002; van den Hoff et al. 2002). For each grid cell, the time (*h*) spent within any grid cell for each individual was calculated. The data were further split into summer and winter to summarize temporal differences in time spent at sea among the oceanographic and fisheries management zones per age group. The seasons were defined by the annual cycle of the juvenile seals: 'summer' was from 1 December to 14 May, and 'winter' from 15 May to 30 November. The 'summer' period starts as the juveniles leave Macquarie Island at the end of their annual moult for their first trip to sea (i.e., encompassing the austral summer). After this period, the rest of the year is defined as 'winter'.

We calculated the time (*h*) spent by each individual within the relevant national exclusive economic zones (EEZ) and CCAMLR-managed areas (Subareas 54.4.1, 88.1 and 88.2). We also did this for five oceanographic/ecological regions defined by major frontal systems within the study area (Orsi et al. 1995; Rintoul et al. 1997). These regions were: (1) Sub-Tropical Zone to the north of the Sub-Tropical Front (STF), (2) Sub-Antarctic Zone (SAZ) between the Sub-Tropical Front and the Sub-Antarctic Front (3) the Polar Frontal Zone (PFZ) between the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (PF), (4) Antarctic Zone (AZ) between the PF and southern boundary of the Antarctic Circumpolar Current (SBDY) including the southern Antarctic Circumpolar Current front (sACCf), and (5) south of the SBDY as the High Antarctic Zone (HAZ).

Population estimates of regional use

Using the daily locations we estimated the total number of seal-days in each of the management regions for the summer and winter periods by estimating the number of individuals within each age group and the mean number of days at sea by those age groups. The number of individuals in each age group was estimated as 10,265 yearlings, 9,808 2-year-olds and 8,033 3-year-olds. These values were derived using a total population of 76,000 seals and assuming a stable age structure for the Macquarie Island population (McMahon et al. 2003).

Results

Over the entire study period, the yearlings spent on average 289.8 ± 11.0 days at sea, the 2-year olds spent 300.2 ± 8.0 days at sea, and the 3-year olds spent 246.3 ± 12.3 days at sea. However, it should be noted that the sample of 3-year olds was biassed towards females attempting to breed for the first time (nine females compared to one male) that had their tracking units removed before their post-breeding trip to sea. If included, this additional trip would have added ~77 ± 1.5 days (Hindell et al. 2003b) to their total time at sea. Yearlings travelled up to 2,296 km from Macquarie Island while ranging from 126°E to 165°W and 41 to 66°S. The 2-year olds travelled up to 5,076 km away, ranging from 115°E to 122°W and 44 to 72°S. The 3-year olds travelled up to 4,084 km away from the island and ranged between 105°E to 123°W and from 43 to 72°S. Overall, the juvenile seals spent less time at sea in the 'summer' period than in the 'winter' period (114 ± 10 and 163 ± 23 days, respectively; Table 1).

Oceanographic/ecological zones

Overall, juvenile seals spent over 95% of their time at sea during the summer period south of the Polar Front (Fig. 1), with the 2- and 3-year olds spending over ~25% of their time in the High Antarctic Zone (Table 2). In winter, juvenile seals spent less time in southern waters, but still spent ~75% of their time south of the Polar Front; the 1- and 2-year-olds spent ~25% in the Sub-Antarctic zone. There was a clear pattern of older seals travelling farther south and farther away from Macquarie Island than younger seals in both summer and winter. However, in winter the 2-year-old seals travelled farther from Macquarie Island mainly in the Sub-Antarctic and Polar Frontal Zones, whereas the 3-year olds did not travel as far but remained in more southerly waters.

Managed areas

There were differences in the amount of time spent within the different management zones (Fig. 2) for each age group (Table 3). In summer, all age groups spent more than ~75% of their time in managed regions. In winter 1- and 2-year-old seals spent over ~65% of their

Table 1 The number of days (mean ± SD) spent at sea by the different age juvenile southern elephant seals from Macquarie Island in summer and winter seasons

Age	*n*	Total		Summer		Winter	
		Mean	SD	Mean	SD	Mean	SD
1	15	289.8	11.0	110.3	7.1	179.5	7.7
2	6	300.2	8.0	127.2	10.4	173.0	11.4
3	10	246.3	12.3	112.9	7.3	133.5	8.4
Overall	31	277.8	24.8	114.4	10.0	163.4	22.7

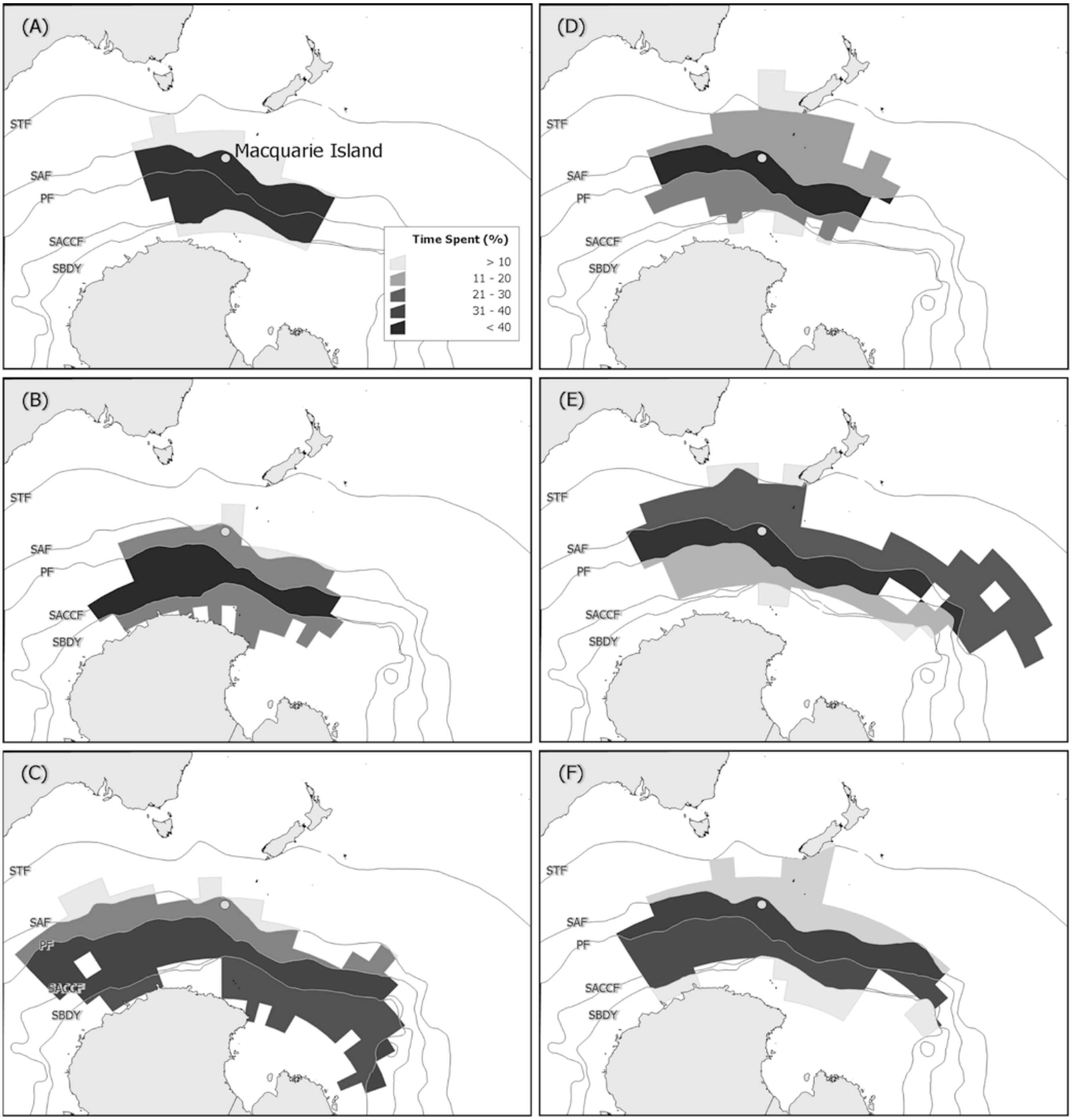

Fig. 1a–f Map showing the proportional time at sea spent in the oceanographic/ecological zones of the Southern Ocean for 1-, 2- and 3-year-old southern elephant seals from Macquarie Island in summer (**a**, **b** and **c**, respectively) and winter (**d**, **e** and **f**, respectively) with *darker shading* indicating more time spent in those regions. Also shown are the mean positions of the oceanographic boundaries of the Southern Ocean (*STF*, *SAF*, *PF*, *sACCf* and the *SBDY*) used to define the oceanographic/ecological zones

time in managed areas, but the 2-year-old seals spent the majority (56%) of their time in the unmanaged high seas. The 1-year olds spent ~50%, and the 2- and 3-year olds spent ~80%, of their time in CCAMLR regions during the summer period. In winter, the amount of time in CCAMLR regions decreased, with the 1- and 2-year olds spending ~30% of their time in the CCAMLR areas; whereas, the 3-year olds remained farther south and spent ~60% of their time in these regions.

The number of seal-days at sea for all juvenile seals (28,108 seals) in the summer and winter periods were 3,286,610 and 4,611,041 days, respectively. In summer, juveniles are estimated to have spent 2,266,297 days in the CCAMLR managed areas, 628,262 days in the unmanaged high seas and 365,532 days in the Australian EEZ (Table 4). In winter, the pattern was different, and

Table 2 The percentage of time spent in the different ecological zones in the summer and winter for the 31 1-, 2- and 3-year-old southern elephant seals in this study. Also shown is the mean time (*h*) ± SD within each zone

Age	Sub-Tropical Zone			Sub-Antarctic Zone			Polar Frontal Zone			Antarctic Zone			High Antarctic Zone		
	Percent	Mean	SD	Percent	Mean	SD	Percent	Mean	SD	Percent	Mean	SD	Percent	Mean	SD
Summer															
1	0.0	0.0	0.0	3.3	89.8	101.9	46.9	1242.6	380.9	46.3	1225.5	430.9	3.5	90.2	145.7
2	0.0	0.0	0.0	0.1	2.8	6.8	25.3	740.2	594.4	50.1	1547.7	541.9	24.6	761.7	630.2
3	0.0	0.0	0.0	1.0	26.1	62.6	24.0	658.4	619.6	39.9	1081.5	585.0	35.0	942.6	785.9
Winter															
1	0.3	14.2	55.0	20.5	885.8	1047.0	54.4	2339.1	827.7	24.6	1061.9	934.3	0.1	5.9	15.9
2	0.6	24.0	48.8	31.4	1318.0	948.0	45.9	1929.1	1163.0	18.2	726.6	974.6	3.9	154.2	327.2
3	0.3	10.5	33.3	12.8	429.0	640.6	41.1	1312.9	806.1	36.6	1161.3	770.9	9.2	289.6	299.1

juveniles are estimated to have spent the most time in the high seas (1,901,839 days), CCAMLR subareas (1,752,738 days) and the remainder of their time in the Australian and New Zealand EEZs (Table 4).

Discussion

Our results show that the juvenile component of the southern elephant seal population at Macquarie Island, though hauling out on a Sub-Antarctic island, spent a large amount of time in managed fisheries areas (especially CCAMLR subareas 54.4.1, 88.1 and 88.2). Although CCAMLR has been successful in the conservative management of the krill-based ecosystem, much of the region has been subject to relatively low harvesting rates (Nicol and Endo 1999; Nicol and Foster 2003), although possible increases in fishing have been predicted (Goldsworthy et al. 2001; Nicol and Foster 2003). At present, the management framework has focused mainly on the krill-based ecosystem south of the sACCF because krill showed the greatest potential for harvesting and they are an important source of food for vertebrate predators (Nicol and Endo 1999; Nicol et al. 2000). The pelagic region, on the other hand, has been more difficult to survey and its importance in terms of potential biomass may have been under-estimated. Indeed, only recently have data become available that reflect the complex community structure and potentially high biomass of secondary producers (Hosie et al. 2004) that support higher-order predators foraging in this region.

Seasonal habitat use

We found a clear pattern in the seasonal use of the Southern Ocean by juvenile elephant seals. In the summer period, juvenile seals spent around 90% of their time south of the Polar Front and 70% within CCAMLR-managed areas. In winter however, juveniles spent the majority (around 75%) of their time between the Polar Front and the southern boundary of the Antarctic Circumpolar Current and ~37% of their time in CCAMLR-managed areas. Our results contrast with the summer use by adult females that spend the majority (46%) of their time in the zone lying between the Sub-Antarctic and Polar Fronts (Hindell et al. 2003b). Additionally, younger seals (8- to 18-month-old) spent only 27% of their time in CCAMLR-managed areas, and ~23% in Australian and New Zealand EEZs (van den Hoff et al. 2002).

Some caution should be exercised when comparing the different spatial use patterns for different age classes. Hindell et al. (2003b) determined that the minimum sample size required to establish 95% coverage of the total area of the ocean used by adult females was 25 individuals. Even though the sample size in our present study represents the largest to date for juvenile seals, our samples sizes were still relatively small, particularly when divided into age and season classes. Thus, our estimates of total area used by the juvenile seals may be underestimated. Despite subtle differences in the timing of at-sea movements for the different age classes, our results nonetheless confirm that juveniles in general appear to use different areas of the Southern Ocean compared to adult females (although there is some overlap).

Oceanographic and ecological habitat use

During both seasons, the juveniles spent much of their time in the Polar frontal and Antarctic zones, which suggest that these regions are important foraging areas. Previously, this region has been considered relatively oligotrophic; however, recent studies have highlighted the high abundance and species richness of zooplankton within these zones (Hosie et al. 2004). Although our understanding of elephant seal diet is still rudimentary (Green and Burton 1993: Slip 1995; Daneri et al. 2000; Santos et al. 2001; Daneri and Carlini 2002; Bradshaw et al. 2003), primary prey species of elephant seals such as squid and fish are thought to depend heavily on zooplankton within this region (Dauby et al. 2003).

Current and potential fisheries overlap

At present there are three commercial fisheries that target known prey of southern elephant seals from

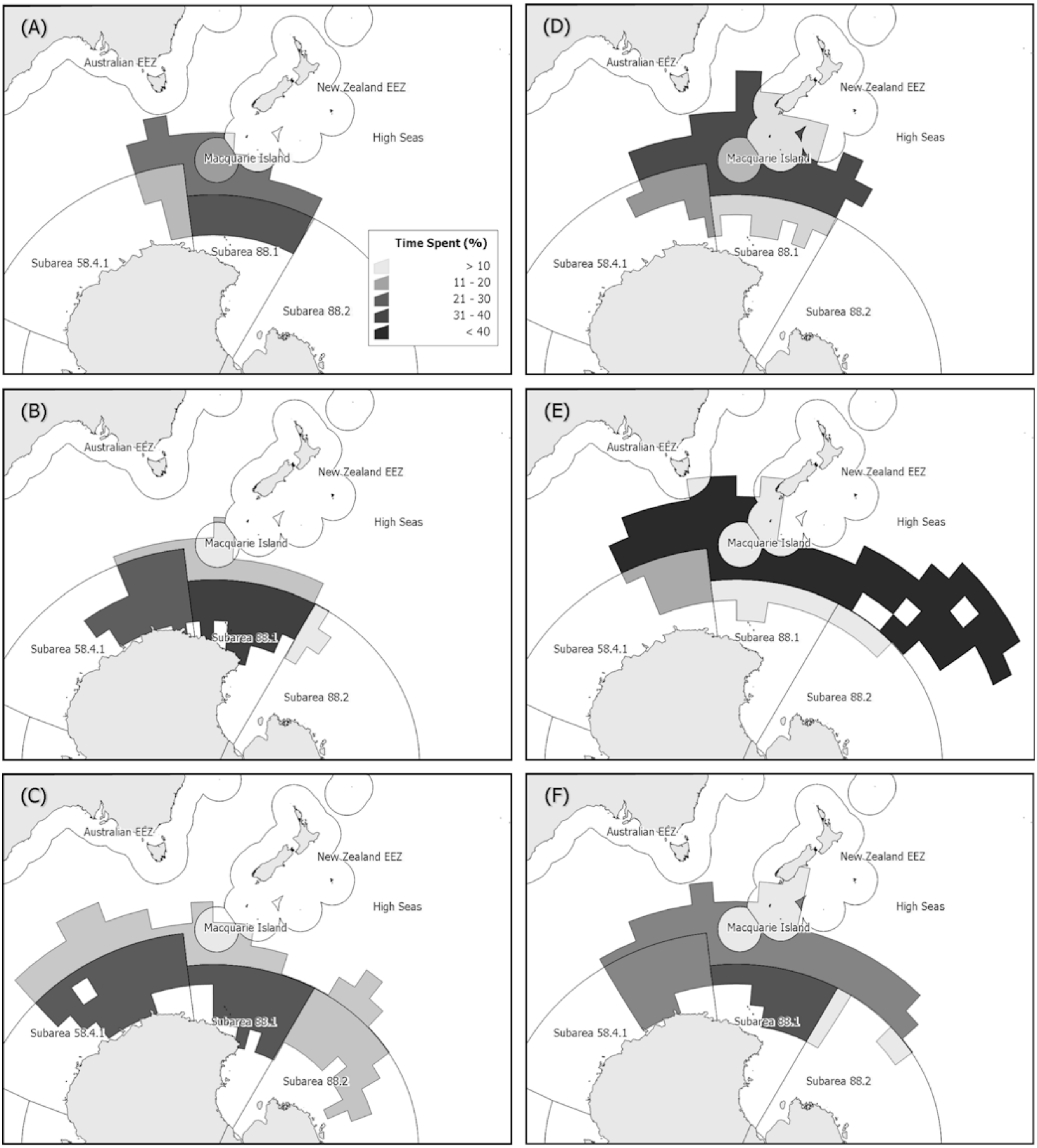

Fig. 2a-f Map showing the proportional time at sea spent in the managed areas (CCAMLR subareas 54.4.3, 88.1 and 88.2 and the 200 nm exclusive economic zone for Australia, Macquarie Island and New Zealand) of the Southern Ocean for 1-, 2- and 3-year-old southern elephant seals from Macquarie Island in summer (**a**, **b** and **c**, respectively) and winter (**d**, **e** and **f**, respectively) with *darker shading* indicating more time spent in those areas

Macquarie Island: (1) Patagonian toothfish (*Dissostichus eleginoides*) have been reported in the diet of elephant seals (Slip 1995; Burton and van den Hoff 2002; I.C. Field, unpublished data) and there are fisheries around Macquarie Island, in the New Zealand EEZ, and in CCAMLR statistical subareas 88.1 and 88.2; (2) The New Zealand squid fishery over the Campbell Plateau; (3) The krill fishery for *E. superba* in CCAMLR statistical subareas 54.4.1, though krill are a minor compo-

Table 3 The proportion of time spent in the different managed areas in the summer and winter for 1-, 2- and 3-year-old southern elephant seals in this study. Also shown is the mean time (*h*) ± SD within each zone

Age	High seas			CCAMLR			Australian EEZ			New Zealand EEZ			Overall managed areas		
	Percent	Mean	SD	Percent	Mean	SD	Percent	Mean	SD	Percent	Mean	SD	Percent	Mean	SD
Summer															
1	26.8	708.6	258.1	50.4	1,334.1	663.6	20.7	548.5	330.0	2.1	56.8	82.1	73.2	1,939.5	523.9
2	16.3	469.0	411.7	77.0	2,383.8	915.2	6.7	199.6	144.6	0.0	0.0	0.0	83.7	2,583.4	742.2
3	14.6	398.9	425.0	79.9	2,155.6	1,001.3	5.3	147.4	117.5	0.3	6.6	20.4	85.4	2,309.6	781.7
Winter															
1	36.8	1,601.1	897.3	34.4	1,487.0	885.2	17.5	733.2	577.6	11.3	485.7	1,001.3	63.2	2,705.9	810.9
2	56.4	2,340.6	1,097.7	27.6	1,147.4	627.0	7.5	311.0	182.5	8.5	352.9	685.3	43.6	1,811.3	528.8
3	24.3	778.3	731.2	61.1	1,935.6	1,011.4	7.4	236.4	165.0	7.1	253.0	623.6	75.7	2,425.0	795.0

Table 4 The estimated total number of seal days spent in the managed fisheries areas by the Macquarie Island population of 1-, 2- and 3-year-old southern elephant seals. Also shown are the population estimates for each age group calculated from a total population of 76,000 seal assuming the stable age structure from McMahon (2003) and the mean number of days at sea for each age group

Age	Number of seals	High seas	Australian EEZ	Macquarie Island EEZ	New Zealand EEZ	Subarea 58-4-1	Subarea 88-1	Subarea 88-2
Summer								
1	10,265	0.0	30,3091.1	234,617.3	24,307.8	189,638.9	380,988.1	0.0
2	9,808	0.0	191,649.2	81,587.2	0.0	373,709.5	516,821.0	83,640.8
3	8,033	0.0	133,522.2	49,327.2	2,210.7	286,855.9	296,719.0	137,923.8
Overall	28,106	0.0	628,262.5	365,531.7	26,518.5	850,204.2	1,194,528.2	221,564.6
Winter								
1	10,265	0.0	684,811.3	313,587.2	207,746.4	400,420.3	235,569.2	0.0
2	9,808	1,504.4	956,528.5	125,588.0	144,229.1	319,463.2	121,820.0	27,611.5
3	8,033	0.0	260,499.4	79,133.1	84,675.5	256,990.0	363,387.0	27,476.5
Overall	28,106	1,504.4	190,1839.1	518,308.3	436,651.0	976,873.5	720,776.2	55,088.0

nent in the diet of southern elephant seals (van den Hoff et al. 2003; Bradshaw et al. 2003). However, if there is expansion of existing fisheries or new resources are found then it is likely that there will be some dietary overlap with this generalist predator that can respond to changes in prey availability (Piatkowski et al. 2002).

Southern elephant seals are major consumers of squid and fish in the Southern Ocean (Clarke 1983; Boyd et al. 1994; Bradshaw et al. 2003; Hindell et al. 2003b), and recent modelling has suggested that elephant seals consume between 19 and 36% of the entire squid biomass taken by all whales, seals and birds combined in the Southern Ocean (Clarke 1983; Santos et al. 2001). The use of conventional techniques (Green and Burton 1993; Slip 1995; van den Hoff et al. 2003) and fatty acid signature analysis (Brown et al. 1999; Bradshaw et al. 2003) have identified that the seals are generalist feeders. A recent study of the diet of adult females has also been able to attribute general feeding patterns relative to different foraging areas (Bradshaw et al. 2003).

Better information on spatial and temporal variation in seal diet combined with detailed, age-specific information on foraging extent and behaviour are needed to improve current models of prey consumption by this apex marine predator. Juvenile southern elephant seals are an important component of the population influencing change in population numbers associated with resource limitations, as found by Trites and Donnelly (2003) in the declining Steller sea lion population of the north Pacific. This, coupled with their wide-ranging at-sea distribution, makes elephant seals a potentially important indicator of both natural and anthropogenic baseline variability within the Southern Ocean marine ecosystem. Thus, elephant seals represent a useful monitoring species for the open ocean pelagic system of the Southern Ocean that will lead to better understanding and management of this poorly described biophysical environment.

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