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Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones

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Summary

1. Numerical models that predict trophic structure require both accurate information on prey consumption rates and estimates of spatial and temporal variation. In the Southern Ocean little information exists on the spatial and temporal patterns of resource use by predators, so we attempted to examine these patterns for an important Antarctic predator, the southern elephant seal. We (i) defined the area of the ocean used by the adult female component of the elephant seal population at Macquarie Island; (ii) quantified the time these seals spent in the different regions of the Southern Ocean; and (iii) estimated the biomass of fish and squid prey consumed per fortnight and per region.

2. We used data from 42 post-breeding females collected from 1992 to 2001. The data consisted of locations determined by geo-location (based on light intensity) recorded using dataloggers. A randomized, incremental analysis of at-sea locations indicated that a sample of 25 individuals was required to provide 95% coverage of the total area of ocean used.

3. The greatest amount of time (44·6%) was spent in the region between the Antarctic Polar Front (APF) and the Subantarctic Front (SAF). Up to 20% of time was spent south of the Antarctic Circle or within Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Statistical Subareas, indicating that seals from Macquarie Island are also important summer-time predators in high Antarctic waters.

4. The adult female population was estimated to consume $122{\cdot}73–125{\cdot}81 \times 10^6$ MJ for the post-lactation foraging trip (31 142–31 925 tonnes of prey). Of this, 47·2–53·4% was consumed within the CCAMLR Statistical Subareas and the Australian and New Zealand exclusive economic zones (EEZ).

5. *Synthesis and applications*. Our study emphasizes that (i) a large sample of individual seals (25) can estimate spatial trends in prey consumption; (ii) much of the estimated prey consumption occurs within fishery-managed zones, therefore elephant seals should be included in models predicting trophic structure in the Southern Ocean; and (iii) recent commercial fishery catch within these zones is minimal relative to the prey consumed by elephant seals, but increases in fishing activity in these zones may result in competition for marine resources.

Key-words: bootstrap models, *Mirounga leonina*, seal management, spatial power

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Introduction

Ocean fisheries' management practices that attempt to understand the relationships between fishing and other top-level predators are often faced with incomplete information (Furness & Tasker 2000; Bjørge *et al.* 2001). This is likely to produce unpredictable outcomes on species occupying the lower trophic levels due to the complicated and largely unpredictable results from altering the population size of secondary producers (Yodzis 2000). This dilemma is particularly pronounced in the Antarctic and Southern Ocean marine ecosystem where there is a low diversity of secondary producer species (such as the Antarctic krill *Euphausia superba*) although these few species occur in vast numbers and are important for the system as a whole (Croxall, Reid & Prince 1999). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is responsible for managing fisheries in the Antarctic region and it attempts to do so from an ecosystem perspective, by maintaining the ecological relationships between harvested, dependent and competing populations (Agnew 1997; Constable *et al.* 2000; Parkes 2000).

Given the complexity of even those systems with low species diversity, such as the Southern Ocean, and the practical difficulties of obtaining data on many of the trophic links, a common approach is to use numerical models to predict trophic structure (Croll & Tershy 1998; Thompson *et al.* 2000). Such models require information on, amongst other things, predator consumption rates, animal abundance, metabolic rates and diet composition. In addition, all ecological data need to be summarized within a spatial and temporal context because the structure of the ocean changes seasonally, annually and regionally.

There have now been numerous studies investigating the space used by Antarctic predators within the Southern Ocean (Boyd 1989; Hindell, Burton & Slip 1991; Field *et al.* 2001; Guinet *et al.* 2001; Weimerskirch *et al.* 2002) and some of these have been used in attempts to model the potential impacts of fisheries on local ecosystems (Thompson *et al.* 2000; Goldsworthy *et al.* 2001). However, most of these studies are based on limited samples in terms of the number of animals tracked and temporal restrictions (i.e. during specific times of the year). There have been no attempts to assess how representative these samples are of the entire population.

Southern elephant seals *Mirounga leonina* (Linnaeus 1758) are numerous, wide-ranging consumers of large quantities of Southern Ocean resources. Santos, Clarke & Pierce (2001) estimated that the total world population of southern elephant seals consumed approximately 4·5 million tonnes of prey (primarily squid) annually (based on a population size of 600 000). This represents 19–36% of the total Antarctic consumption of cephalopods by sperm whales, beaked whales, seals and seabirds combined (Clarke 1983). Southern elephant seals also range widely and feed within the economic exclusion zones (EEZ) of several nations (e.g. Argentina, Australia and New Zealand), as well as within the regions of the Southern Ocean managed by CCAMLR (Hindell, Burton & Slip 1991; Campagna *et al.* 1995; Lewis, Campagna & Quintana 1996; McConnell & Fedak 1996).

There have been many studies on the diet, behaviour and spatial use of southern elephant seals (Hindell, Burton & Slip 1991; Rodhouse *et al.* 1992; Green & Burton 1993; Slip 1995) that provide potentially important input parameters for ecosystem models. However, as with many other Southern Ocean predators, different age and sex classes of southern elephant seals can differ in their spatial and temporal patterns of feeding (Hindell, Burton & Slip 1991; McConnell & Fedak 1996; Hindell *et al.* 1999; Field *et al.* 2001; Bradshaw *et al.* 2002; van den Hoff *et al.* 2002). This makes it necessary to quantify and model these components separately to form a complete population model.

The Macquarie Island population of southern elephant seals has been studied since the 1950s (Carrick & Ingham 1960) and has received particular attention over the last decade largely in response to the need to understand the on-going decline in population size (Hindell 1991; Hindell, Burton & Slip 1991; Hindell, Slip & Burton 1991; Hindell, Slip & Burton 1994; Slip, Hindell & Burton 1994; Hindell & Slip 1997). An important aspect of this research has been to quantify the at-sea movements of the seals, and now these data provide a sufficiently large sample of animals to address the representativeness of the foraging data relative to the breeding female population.

The specific aims of this study were therefore to: (i) determine the sample of individual seals required to provide a reliable indication of the regions of the ocean used by the adult female component of the Macquarie Island population during summer; (ii) quantify the time that these seals spend in the different regions of the Southern Ocean with respect to management zones, and with respect to ecological zones delimited by oceanographic features; and (iii) construct a simple model to estimate the potential summer prey consumption within these political and ecological zones.

Materials and methods

DATA COLLECTION

Since 1990, 42 separate adult female southern elephant seals have been fitted with time-depth recorder archival tags (TDR; Wildlife Computers, Seattle, WA, USA) at Macquarie Island (54°35′S, 158°55′E). For each individual, we only selected the first TDR record because many had multiple TDR deployments. The TDR sampled time, depth, light level and temperature every 30 s for the duration of the 10-week post-lactation foraging trip. The details of how the units were attached, how the data were retrieved and summarized, and how the

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locations were determined have been presented elsewhere (Hindell & Slip 1997; Bradshaw *et al*. 2002).

The resulting locations were filtered to exclude any falling outside a maximum velocity of 300 km day^{-1} (12·5 km h^{-1}) (Bradshaw *et al*. 2002). Once filtered, the tracks for each seal were divided into seven fortnightly intervals beginning from 16 October 1999 and continuing to 31 January 2000. We summarized these locations by creating a raster grid with cells of 350 × 350 km (Bradshaw *et al*. 2002).

MINIMUM SAMPLE REQUIRED

There are several techniques used to calculate the minimum number of location fixes required to estimate an individual's use of its environment adequately. A conventional approach is to collect enough fixes so that the addition of subsequent fixes does not expand the range area significantly (White & Garrott 1990). We adopted a similar logic, but used the number of individuals within the population as opposed to the number of geographical positions obtained per individual.

We initially selected, at random, one of the 42 seals and calculated the total area of ocean used by this seal by summing the number of grid cells used during its post-lactation foraging trip. From the seals remaining in the sample, we selected a second one at random and recalculated the sum of the area used by both seals. We repeated this procedure until all 42 seals were included in the calculation of total area. We then used a Monte Carlo bootstrap technique to estimate mean use and the associated variance (Manly 1997; Chernick 1999). We repeated the above process 10 000 times, calculating the area occupied by j seals, plus the associated standard error ($\hat{\sigma}_{boot}$):

$$\hat{\sigma}_{boot} = \sqrt{\frac{n-1}{n}}\left(\sqrt{\frac{1}{n(n-1)}\sum_{i=1}^{n}(x_i - \bar{x}_j)^2}\right) \qquad \text{eqn 1}$$

where n = the number of iterations, $\bar{x}$ = the mean area occupied by j seals, and x_i = the area occupied by the j^{th} seal at iteration i (Chernick 1999). Thus, different seals were chosen at random for each of the 10 000 iterations.

The resulting curve was examined for evidence of an asymptote within the sample of 42 seals, which could be taken as evidence for a maximum area occupied by j seals. For example, if there was no significant increase in total area occupied after 20 seals were included in the sample, this could be taken as evidence that, on average, 20 randomly selected adult female seals from the Macquarie Island population would estimate the total spatial extent occupied by the population of adult females.

We also expressed these data in terms of the total potential ocean area available to the seals, by projecting a maximum distance radius from Macquarie Island based on mean and maximum rates of travel observed for this species (McConnell & Fedak 1996). These were:

Radius 1 – mean: 79·4 km day^{-1} × 0·5(101 days) = 4009·7 km

Radius 2 – maximum: 115·0 km day^{-1} × 0·5(101 days) = 5807·5 km

where 101 days represents the longest post-lactation foraging trip observed for the sample of 42 TDR records used in the analysis (Table 1).

All radii were extended from Macquarie Island based on a Azimuthal Equidistant map projection (Gudmundsson & Alerstam 1998). However, that projection does not conserve area over broad spatial scales; therefore, we transformed the resulting circles into a Lambert Azimuthal projection. All land areas (e.g. Australia, New Zealand, Antarctica) falling within these radii was excluded from the estimates of total area.

SPATIAL AND TEMPORAL ALLOCATION OF TIME SPENT AT SEA

Using a second Monte Carlo bootstrap, we calculated the mean number of seal hours in each 350 × 350-km grid cell and their standard errors. This technique involved selecting 42 seal records at random with replacement from the sample available (Chernick 1999). The number of hours that these sampled seals spent in each grid cell and the coordinates of the cells themselves were retained. This process was repeated 10 000 times to produce 10 000 possible scenarios of seal use. The mean number of hours per grid cell and its standard error were calculated following the method outlined above (Chernick 1999). We also divided the

Table 1. Details of the 42 TDR deployed on post-lactation female southern elephant seals at Macquarie Island between 1990 and 1999

Year	Number of deployments	Type of TDR	Maximum days at sea
1990	4	Mk3	59
1993	6	Mk3	70
1995	4	Mk3	77
1996	6	Mk3 + Mk6	80
1997	2	Mk3 + Mk6	55
1999	17	Mk6 + Mk7	99
2000	3	Mk6 + Mk7	101
Total	42	–	–

data into seven fortnightly intervals, from the last fortnight in October through to the last fortnight in January. The bootstrap method with replacement was used to calculate the mean number of seal hours (and standard error) for each grid cell for each fortnightly interval. These values were also expressed as proportions of the total mean seal hours spent at sea.

FISHERIES MANAGEMENT AREAS AND OCEANOGRAPHIC ZONES

We separated the total number of seal hours, and the relative proportion of time spent, into each of the three CCAMLR Statistical Subareas (58·4·1, 88·1 and 88·2), as well as the Macquarie Island (Australian) and New Zealand 200-nautical mile EEZ. We defined a grid cell as falling within a particular zone when ≥ 50% of the grid cell fell within that zone.

We also calculated the overlap between grid cells and the following four oceanographic regions: (i) south of the southern limit of the Antarctic Circumpolar Current (SACC); (ii) between the SACC and the Antarctic Polar Front (APF); (iii) between the APF and the Subantarctic Front (SAF); and (iv) north of the SAF. The limits of these frontal zones were defined as the average position of these fronts compiled from all historical hydrographic stations collected prior to and including 1990 (Orsi, Whitworth & Nowlin 1995).

SPATIAL COMPONENTS OF ENERGY CONSUMPTION

We estimated prey consumption by seals for each of the fisheries management and ecological zones using a simple energetic model based on Goldsworthy *et al.* (2001). First we calculated the number of hours spent by all seals in each 350 × 350-km grid cell. This was based on the results of the bootstrap analysis where the average proportion of time that the sample of 42 seals spent in each cell was calculated. These proportions were then converted to the total number of seal days per cell based on the estimated population of 20 300 adult female elephant seals at Macquarie Island (Goldsworthy *et al.* 2001). We multiplied the number of seal days per grid cell by the at-sea field metabolic rate of 101 MJ day^{-1} $seal^{-1}$ (Hindell & Lea 1998) to derive an estimate of the total energy consumption per cell.

We then converted total energy consumption per cell into total mass of prey consumed. For this we assumed an average diet composition of 55% squid and 45% fish (Slip 1997b), with a mean energy density of 3·645 kJ g^{-1} and 6·518 kJ g^{-1}, respectively, and an overall energy assimilation rate of 75% (Boyd, Arnbom & Fedak 1994; Goldsworthy *et al.* 2001). Although Boyd, Arnbom & Fedak (1994) suggested an alternative diet composition of 75% squid and 25% fish, they conceded that fish were probably underrepresented in stomach flushes. We therefore used an estimation of dietary composition that is richer in fish (Slip 1997b).

Results

MINIMUM SAMPLE REQUIRED

The curve for the number of grid cells used with increasing number of seals exhibited a clear asymptote (Fig. 1). To test whether the asymptotic form of the curve was a true reflection of the relationship rather

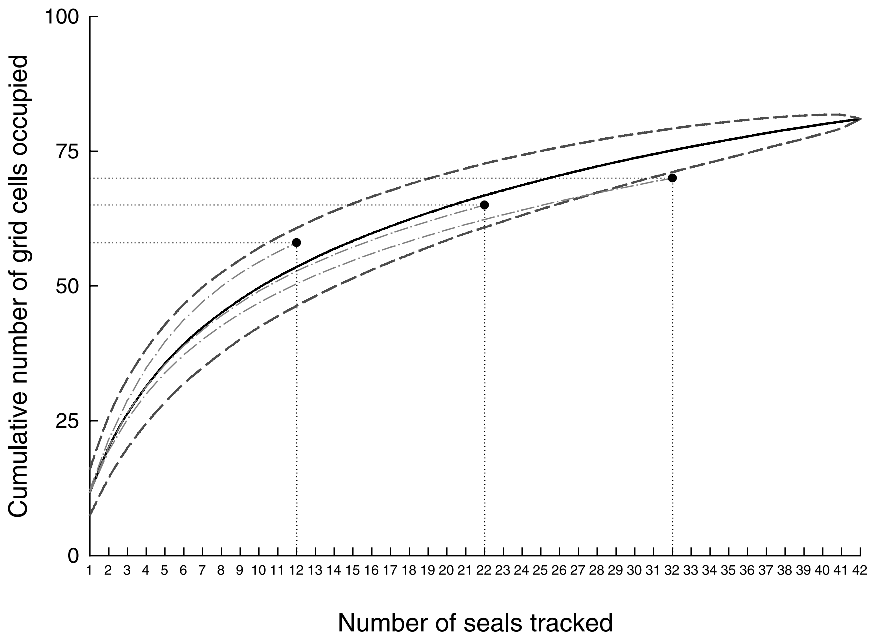

Fig. 1. The mean and standard deviation of the cumulative number of grid cells occupied by adult female southern elephant seals during the post-lactation foraging trip relative to sample size (i.e. number of individuals tracked). Also shown are three subsamples of 12, 22 and 32 seals for which the cumulative cells occupied curves were recalculated. These demonstrate that the general asymptotic form of the curve remains unchanged despite the initial sample used.

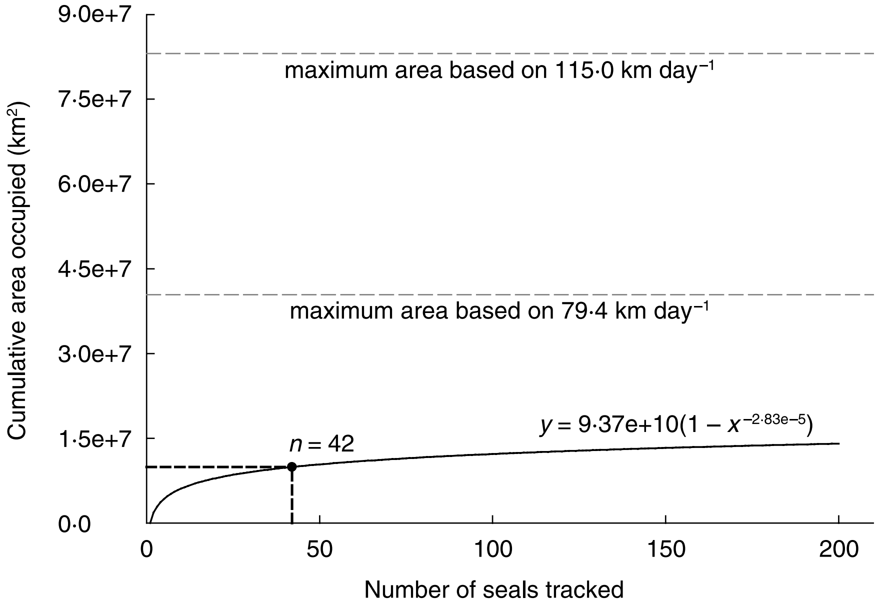

Fig. 2. Cumulative area occupied relative to number of individual seals tracked for the total sample (42 individuals) and the extrapolated sample of 200 individuals. The curve is best described by the power function of the form $\text{area}_{cumulative} = a(1 - x^{-b})$. Also shown are the potential maximum attainable areas achievable based on the mean and maximum swimming velocity radii (79·4 km day^{-1}, 115·0 km day^{-1}).

than an artefact of the bootstrap method, we calculated separate curves for randomly selected samples consisting of 12, 22 and 32 seals, and recalculated the curve. All of these subsample curves fell within approximately 1 SD of the mean values generated from the entire sample. This corroborates the general form of the curve because a small sample of seals (12 seals) did not exhibit an asymptote (Fig. 1).

We plotted the total area occupied vs. the number of seals tracked (corrected for area bias by multiplying the cosine of latitude for each grid cell and the grid cell area of 350 × 350 km) as:

$$\text{area}_{cumulative} = a(1 - x^{-b})$$

where $a = 9{\cdot}37 \times 10^{10}$ and $b = 2{\cdot}83 \times 10^{-5}$ ($r^2 > 0{\cdot}999$, $F_{1,40} = 252402{\cdot}6$, $P \ll 0{\cdot}0001$).

We extended the maximum area occupied predicted from the power function to 200 seals and compared this with the maximum areas calculated from the maximum velocity radii (Figs 2 and 3). This suggests that 42 seals provided a realistic estimate of the total area used by the adult female seal population at Macquarie Island. Further, the asymptote was considerably lower than the maximal areas calculated from the mean and maximum velocity radii (23·2% of area from radius 1; 11·3% of area from radius 2; Fig. 2), indicating a high degree of selection of specific ocean regions largely to the south and east of Macquarie Island.

SPATIAL AND TEMPORAL ALLOCATION OF TIME SPENT AT SEA

The seals spent an average of 77·3 ± 1·5 days (mean ± SE) at sea and ranged from 125°E to 140°W longitude and 45°S to 67°S latitude (Fig. 3). The amounts of time spent in the various zones over each fortnightly period were highly variable (Tables 2 and 3). Dispersion was least in late October and again in late January, because these were periods spent travelling to and from foraging areas. Dispersion was greatest in November and early December, when most seals were evidently in foraging areas.

TIME SPENT IN FISHERY MANAGEMENT AREAS

Twenty-seven per cent of the seals' time was spent in CCAMLR Statistical Subareas 88·1, 88·2 and 58·4·1, and 23·3% of the time was spent in the Australian EEZ for Australia and New Zealand (Table 2). The remaining 49·7% of time was spent outside management zones. CCAMLR Subarea 88·1 was used the most (21·8% time spent at sea). Approximately equal amounts of time were spent in Australian (10·4%) and New Zealand (13%) EEZ.

The amount of time spent in each management zone also varied widely between fortnights (Table 2). In late October (only 439·5 seal hours recorded) most seals had not yet left Macquarie Island, or had only just departed, and were therefore still within the Australian EEZ. During November and December the proportion of time spent in the CCAMLR Subareas remained fairly consistent, although there was considerable variation in the time spent in the EEZs (Table 2).

TIME SPENT IN OCEANOGRAPHIC ZONES

Seals spent most of their time at sea (44·6%) between the SAF and APF (Table 3 and Fig. 3). Some 31·6% of their time was spent north of the SAF, 19·7% between

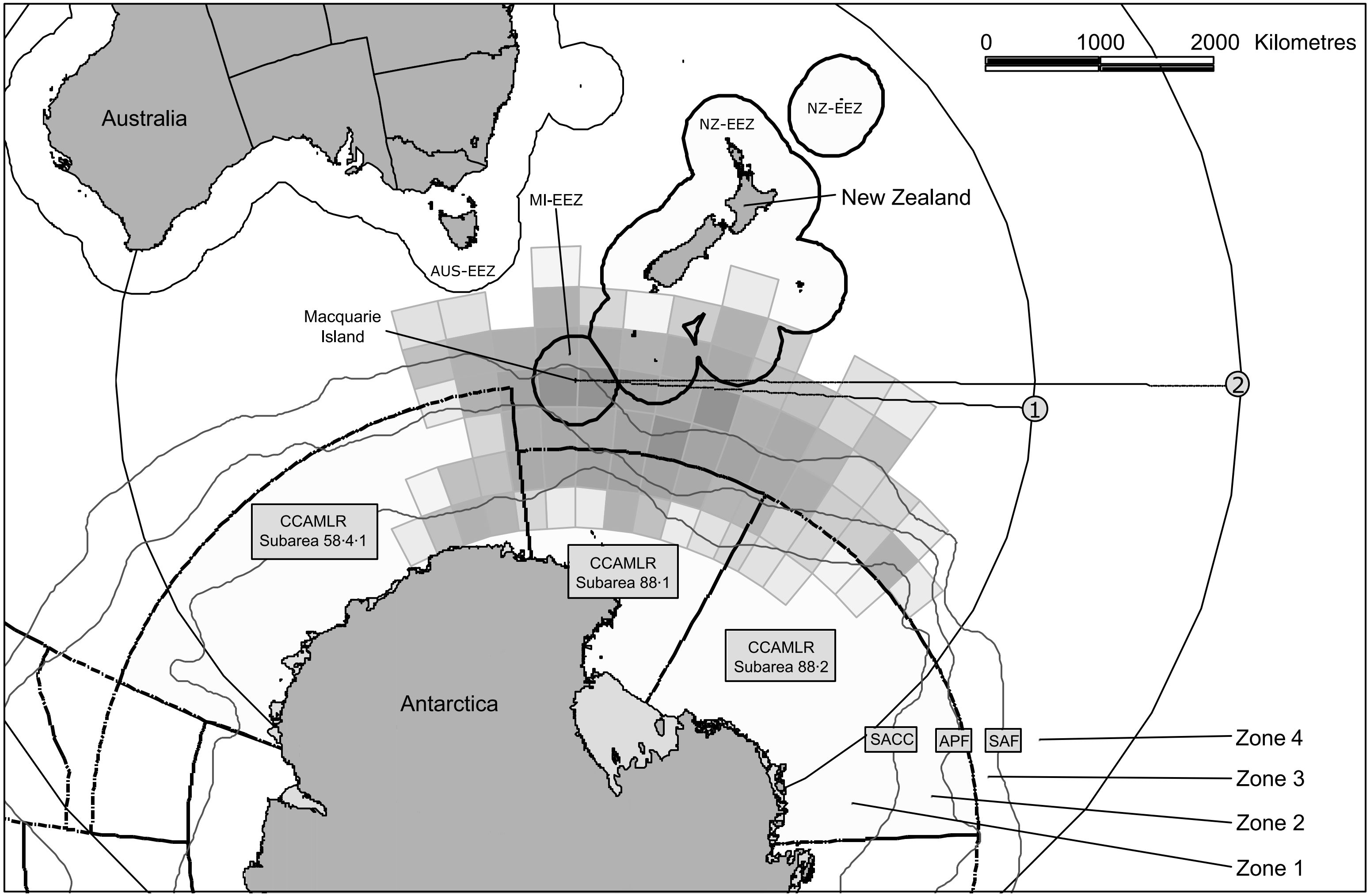

Fig. 3. Map showing political (CCAMLR Subareas 58·4·1, 88·1 and 88·2, and the 200-nm EEZ for Australia/Macquarie Island and New Zealand) and oceanographic boundaries (SAF, APF, SACC) used to define oceanographic zones (zones 1–4) used in the analysis. Also shown in 350 × 350-km grid cells is the time spent by breeding adult female southern elephant seals. Darker cells indicate more time spent in those cells (Bradshaw *et al.* 2002). Mean and maximum velocity radii for the calculation of maximum spatial extent possible are also shown (radius 1 = 4009·7 km; radius 2 = 5807·5 km). Map coordinates projected using the Azimuthal Equidistant projection.

Table 2. The mean proportion of total time each fortnight spent in each of the fishery management zones derived from the bootstrap analysis of 42 post-lactating southern elephant seals. Also shown is the mean total time (h) that the seals spent at sea for each fortnightly period from mid-October (Oct2) to the end of January (Jan2). The numbers following the month abbreviations indicate either the first (1) or second (2) fortnight of that month

		Fortnightly period							
		Oct1	Nov1	Nov2	Dec1	Dec2	Jan1	Jan2	Overall
CCAMLR Statistical Subareas	88·1	0·5	13·3	16·9	17·1	22·6	28·8	36·0	21·8
	88·2	–	0·3	1·0	2·6	–	–	–	0·7
	58·4·1	0·9	1·7	6·9	6·8	3·9	1·8	0·3	4·6
	Total	1·4	15·3	24·9	26·4	26·6	30·6	36·3	27·0
EEZ	Australia	12·3	18·0	7·0	4·2	5·0	19·8	23·9	10·4
	New Zealand	37·4	18·7	4·9	11·6	15·0	15·9	12·7	13·0
	Total	49·7	36·7	11·9	15·7	19·9	35·8	36·6	23·3
Combined management zones		51·1	52·0	36·8	42·1	46·5	66·4	72·9	50·3
Total time (h)		439·5	10659·3	12598·0	12976·2	12864·3	7761·6	2616·2	73108·5

Table 3. The mean proportion of total time each fortnight spent (from mid-October, Oct2, to the end of January, Jan2) in each of the oceanographic zones (Antarctic Circumpolar Current, ACC; Antarctic Polar Front, APF; Subantarctic Front, SAF) derived from the bootstrap analysis of 42 post-lactating southern elephant seals. Also shown is the mean total time (h) that the seals spent at sea for each fortnightly period. The numbers following the month abbreviations indicate either the first (1) or second (2) fortnight of that month

	Fortnightly period							
Ecological zone	Oct2	Nov1	Nov2	Dec1	Dec2	Jan1	Jan2	Overall
1 South of ACC	–	1·6	7·3	3·8	3·9	1·4	12·7	4·1
2 ACC–APF	4·7	16·1	19·1	26·8	21·9	21·7	31·7	19·7
3 APF–SAF	14·0	38·2	36·6	38·0	43·4	54·8	26·1	44·6
4 North of SAF	81·4	43·8	35·7	30·9	30·7	21·1	29·5	31·6

the APF and SACC, while only 4·1% was spent south of the SACC. As might be expected, seals spent a considerable portion (81·4%) of the first fortnight in the northern-most zone. This was not the case for the last fortnight, probably reflecting a few individuals who lingered in this zone prior to returning to Macquarie Island. Except for late January, seals spent little time (1·4–7·3%) in the southern-most zone. In the next most southerly zone (zone 2), the time spent ranged from 16·1% to 31·7% (excluding late October). Zone 3 exhibited the highest usage in four of the seven fortnightly periods, ranging from 36·6% to 54·8%. The most northerly zone (zone 4) was the most important during three of the seven fortnightly periods (late October and early November, and in late January).

Spatial components of prey consumption

Estimates of total energy consumption are presented in Tables 4 and 5, and the corresponding estimates of total fish and squid prey consumption are presented in Tables 6 and 7. We estimate that the adult female population at Macquarie Island consumes 122·73–125·81 × 10^6 MJ during the post-lactation foraging trip (Table 5), accounting for 13 886–14 236 tonnes of fish and 17 256–17 690 tonnes of squid (Table 7). Approximately 15 078–16 639 tonnes (i.e. 47·2–53·4%) were consumed in the management zones (Table 6), but mostly within the three CCAMLR Statistical Subareas. Prey consumption within these CCAMLR Subareas was 7801–9193 tonnes, which equates to 6·2–13·5% of their total post-lactation prey consumption (Table 6).

Because most time was spent between the APF and SAF, most prey was consumed in this zone (12 673–12 953 tonnes), followed closely by the zone lying to the north of the SAF (10 398–10 662 tonnes). Only 1315 and 1363 tonnes of prey were eaten in the most southerly and least-visited zone (Table 7).

Discussion

Minimum sample required

We determined with reasonable accuracy (95%) the number of seals required to give a useful representation of the spatial extent achieved by the population of adult female southern elephant seals from Macquarie Island. The relative increase in the relationship between area occupied and the number of seals tracked diminished substantially after approximately 25 individuals. Therefore, studies investigating the southern elephant seal foraging behaviour and extent should

Table 4. The total number of seal days and energy consumption by the estimated population of 20 300 female, post-lactation southern elephant seals from Macquarie Island. The data are divided into fortnightly periods from mid-October (Oct2) to the end of January (Jan2) and presented for the three management regions in the area. All data are expressed as lower and upper 95% confidence ranges of time spent in each 350 × 350-km grid cell based on SE calculated by the bootstrap analysis using 10 000 randomizations. The numbers following the month abbreviations indicate either the first (1) or second (2) fortnight of that month

	Management region			
Fortnightly period	CCAMLR	Australian EEZ	New Zealand EEZ	Overall
Seal days (× 10^3)				
Oct2	0·11–0·14	0·83–1·21	3·15–3·68	4·08–5·03
Nov1	33·20–34·14	39·31–39·86	40·65–41·38	113·17–115·38
Nov2	64·27–66·14	17·85–18·31	12·43–12·78	94·55–97·23
Dec1	69·72–71·71	10·96–11·28	30·29–31·20	110·97–114·18
Dec2	69·27–71·21	13·10–13·33	39·19–39·97	121·55–124·52
Jan1	48·63–49·86	31·50–31·94	25·12–25·66	105·25–107·45
Jan2	19·18–19·85	12·78–13·01	6·78–6·92	38·74–39·78
Total	304·38–313·05	126·32–128·94	157·61–161·59	588·31–603·57
Total energy consumption (MJ × 10^6)				
Oct2	0·011–0·014	0·08–0·12	0·32–0·37	0·41–0·51
Nov1	3·35–3·45	3·97–4·03	4·11–4·18	11·43–11·65
Nov2	6·49–6·68	1·80–1·85	1·26–1·29	9·55–9·82
Dec1	7·04–7·24	1·11–1·14	3·06–3·15	11·21–11·53
Dec2	7·00–7·19	1·32–1·35	3·96–4·04	12·28–12·58
Jan1	4·91–5·04	3·18–3·23	2·54–2·59	10·63–10·85
Jan2	1·94–2·00	1·29–1·31	0·69–0·70	3·91–4·02
Total	30·74–31·62	12·76–13·02	15·92–16·32	59·42–60·96

Table 5. The number of seal days that 20 300 post-lactation southern elephant seals spent in each of the ecological zones for each fortnightly period between mid-October (Oct2) and the end of January (Jan2). Also listed are the total energy consumption and estimated prey consumption for each zone. All data are expressed as lower and upper 95% confidence ranges for the proportion of time spent in each 350 × 350-km grid cell based on SE calculated by the bootstrap analysis using 10 000 randomizations. The numbers following the month abbreviations indicate either the first (1) or second (2) fortnight of that month

	Ecological zone				
Fortnightly period	Zone 1	Zone 2	Zone 3	Zone 4	Overall
Seal days (× 10^3)					
Oct2	–	0·34–0·50	1·00–1·52	6·86–7·82	8·20–9·85
Nov1	3·35–3·49	34·88–35·87	83·15–84·78	95·19–97·08	216·57–221·22
Nov2	18·94–19·57	49·33–50·63	94·90–97·03	92·30–94·72	255·47–261·95
Dec1	10·05–10·43	70·73–72·66	100·53–103·03	81·65–83·85	262·96–269·99
Dec2	10·10–10·50	57·08–58·60	113·53–115·97	80·42–82·16	261·13–267·23
Jan1	2·14–2·22	34·50–35·47	87·51–88·93	33·62–34·38	157·77–267·23
Jan2	6·71–6·98	16·78–17·30	13·86–14·15	15·66–16·02	53·00–54·45
Total	51·29–53·20	263·65–271·04	494·47–505·42	405·70–416·02	1215·12–1245·68
Total energy consumption (MJ × 10^6)					
Oct2	–	0·03–0·05	0·10–0·15	0·69–0·79	0·83–0·99
Nov1	0·34–0·35	3·52–3·62	8·40–8·56	9·61–9·80	21·87–22·34
Nov2	1·91–1·98	4·98–5·11	9·58–9·80	9·32–9·57	25·80–26·46
Dec1	1·02–1·05	7·14–7·34	10·15–10·41	8·25–8·47	26·56–27·29
Dec2	1·02–1·06	5·77–5·92	11·47–11·71	8·12–8·30	26·34–26·99
Jan1	0·22–0·22	3·48–3·58	8·84–8·98	3·40–3·47	15·94–16·26
Jan2	0·68–0·70	1·69–1·75	1·40–1·43	1·58–1·62	5·35–5·50
Total	5·18–5·37	26·62–27·37	49·94–51·05	40·98–42·02	122·73–125·81

strive to have a minimum sample of 25 individuals to estimate the population response.

This is the first study that has attempted to put spatial data collected for a large ocean predator into the context of a population-level response rather than documenting individual behaviour. This is because (i) we employed a robust statistical technique (bootstrapping) that estimated the minimum sample required to record maximum spatial dispersion, and (ii) we had collected a sufficient number of foraging records to estimate a biologically and statistically meaningful result. Many previous studies, often constrained by logistic difficulties, have documented individual behaviour in top-level ocean predators and then extrapolated

Table 6. The total amount of squid and fish prey consumed by 20 300 post-lactation southern elephant seals from Macquarie Island. The data are divided into fortnightly periods from mid-October (Oct2) to the end of January (Jan2), and presented for the three management regions in the area. All data are expressed as lower and upper 95% confidence ranges based on SE calculated for the proportion of time spent in each 350 × 350-km grid cell based on SE calculated by the bootstrap analysis using 10 000 randomizations. The numbers following the month abbreviations indicate either the first (1) or second (2) fortnight of that month

	Management region			
Fortnightly period	CCAMLR	Australian EEZ	New Zealand EEZ	Overall
Squid consumed (× 10^3 tonnes)				
Oct2	0·002–0·003	0·012–0·017	0·045–0·052	0·058–0·072
Nov1	0·472–0·650	0·558–0·566	0·577–0·588	1·607–1·804
Nov2	0·913–1·260	0·253–0·260	0·176–0·182	1·343–1·702
Dec1	0·990–1·018	0·156–0·160	0·430–0·443	1·576–1·622
Dec2	0·984–1·357	0·186–0·189	0·556–0·568	1·726–2·114
Jan1	0·691–0·950	0·447–0·454	0·357–0·364	1·495–1·768
Jan2	0·272–0·378	0·182–0·185	0·096–0·098	0·550–0·661
Total	4·322–5·616	1·794–1·831	2·238–2·295	8·335–9·742
Fish consumed (× 10^3 tonnes)				
Oct2	0·001–0·002	0·009–0·014	0·036–0·042	0·047–0·058
Nov1	0·379–0·390	0·449–0·456	0·465–0·473	1·293–1·319
Nov2	0·735–0·756	0·204–0·209	0·142–0·146	1·081–1·111
Dec1	0·797–0·819	0·125–0·129	0·346–0·357	1·268–1·305
Dec2	0·792–0·814	0·150–0·152	0·448–0·457	1·389–1·423
Jan1	0·556–0·570	0·306–0·365	0·287–0·293	1·203–1·228
Jan2	0·219–0·227	0·146–0·149	0·078–0·09	0·443–0·455
Total	3·478–3·577	1·444–1·474	1·801–1·847	6·723–6·898
Total prey consumed (× 10^3 tonnes)				
Oct2	0·0003–0·004	0·021–0·031	0·081–0·094	0·105–0·130
Nov1	0·851–1·041	1·008–1·022	1·042–1·060	2·900–3·123
Nov2	1·647–2·016	0·457–0·469	0·319–0·328	2·423–2·813
Dec1	1·787–1·838	0·281–0·289	0·776–0·800	2·844–2·926
Dec2	1·787–2·170	0·336–0·342	1·004–1·024	3·115–3·537
Jan1	1·246–1·520	0·807–0·818	0·644–0·658	2·697–2·996
Jan2	0·491–0·605	0·328–0·333	0·174–0·177	0·993–1·116
Total	7·801–9·193	3·237–3·305	4·039–4·141	15·078–16·639

their findings to population-level conclusions (elephant seals: Le Boeuf *et al*. 2000; Field *et al*. 2001; Antarctic fur seals: Boyd 1989; New Zealand fur seals: Harcourt *et al*. 2002; albatrosses: Brothers *et al*. 1998; penguins: Bost *et al*. 1997). The procedure employed in this study provides a means of assessing the validity of such extrapolations, and is particularly important when the data are to be incorporated into prey-consumption models.

Although the conclusions are robust due to the non-distributional bootstrap method (Manly 1997), we assumed that the relationship between area occupied and the number of seals sampled followed a simple power function. The representativeness of this function to predict maximum spatial coverage beyond the true sample size needs to be tested further through the addition of more data (i.e. more seals tracked) before further conclusions can be drawn.

OCEANOGRAPHIC ZONES

Female southern elephant seals from Macquarie Island do not forage randomly, being found predominantly between the APF and the SAF (Table 3) during the post-lactation foraging trip. This area (zone 3) also appears to be of importance for other top predators of the Southern Ocean (Hull, Hindell & Michael 1997; Hull 1999; Field *et al*. 2001) and may show greater productivity than surrounding areas given the strong thermal structure associated with these waters (Rintoul, Donguy & Roemmich 1997; Moore & Abbott 2002). While we have estimated the dispersion and prey consumption of southern elephant seals relative to oceanographic zones, further studies of these zones, particularly of their biological communities, would be especially enlightening. In addition, elephant seals from Macquarie Island are known to spend a much higher proportion of their time at sea in the zone south of the SACC (zone 1) during winter (Slip, Hindell & Burton 1994; M. Hindell and C. Bradshaw, unpublished data), so further research is required to calculate the prey consumption in that area during that time.

PREY CONSUMPTION AND FISHERY MANAGEMENT AREAS

Recent studies of foraging zones of elephant seals have indicated that they range widely from their subantarctic breeding sites, even to the extent that they enter and forage within high-latitude waters surrounding

Table 7. The number of seal days that 20 300 post-lactation southern elephant seals spent in each of the ecological zones for each fortnightly period between mid-October (Oct2) and the end of January (Jan2). Also listed are the total energy consumption and estimated prey consumption for each zone. All data are expressed as lower and upper 95% confidence ranges for the proportion of time spent in each 350 × 350-km grid cell based on SE calculated by the bootstrap analysis using 10 000 randomizations. The numbers following the month abbreviations indicate either the first (1) or second (2) fortnight of that month

	Ecological zone				
Fortnightly period	Zone 1	Zone 2	Zone 3	Zone 4	Overall
Squid consumed (× 1000 tonnes)					
Oct2	–	0·005–0·007	0·014–0·022	0·097–1·111	0·116–0·140
Nov1	0·048–0·050	0·495–0·509	1·181–1·204	1·352–1·379	3·076–3·142
Nov2	0·269–0·278	0·701–0·719	1·348–1·378	1·311–1·345	3·628–3·720
Dec1	0·143–0·148	1·005–1·032	1·428–1·463	1·159–1·191	3·734–3·834
Dec2	0·143–0·149	0·811–0·832	1·612–1·647	1·142–1·167	3·708–3·795
Jan1	0·030–0·032	0·490–0·504	1·243–1·263	0·477–0·488	2·241–2·286
Jan2	0·095–0·99	0·238–0·246	0·197–0·201	0·222–0·227	0·753–0·773
Total	0·728–0·755	3·744–3·849	7·022–7·177	5·761–5·908	17·256–17·690
Fish consumed (× 1000 tonnes)					
Oct2	–	0·004–0·006	0·011–0·017	0·078–0·089	0·094–0·113
Nov1	0·038–0·040	0·399–0·410	0·950–0·969	1·088–1·109	2·475–2·528
Nov2	0·216–0·224	0·564–0·579	1·084–1·109	1·055–1·082	2·919–2·994
Dec1	0·115–0·119	0·808–0·830	1·149–1·177	0·933–0·958	3·005–3·085
Dec2	0·115–0·120	0·652–0·670	1·297–1·325	0·919–0·939	2·984–5·054
Jan1	0·024–0·025	0·394–0·405	1·000–1·016	0·384–0·393	1·803–1·840
Jan2	0·077–0·080	0·192–0·198	0·158–0·162	0·179–0·183	0·606–0·622
Total	0·586–0·608	3·013–3·097	5·651–5·776	4·636–4·754	13·886–14·236
Total prey consumed (× 1000 tonnes)					
Oct2	–	0·009–0·013	0·026–0·039	0·176–0·201	0·210–0·252
Nov1	0·086–0·089	0·894–0·919	2·131–2·173	2·440–2·488	5·551–5·670
Nov2	0·485–0·502	1·264–1·298	2·432–2·487	2·366–2·427	6·547–6·713
Dec1	0·259–0·267	1·813–1·862	2·576–2·641	2·093–2·149	6·739–6·919
Dec2	0·259–0·269	1·463–1·502	2·910–2·972	2·061–2·106	6·692–6·849
Jan1	0·055–0·057	0·884–0·909	2·243–2·279	0·862–0·881	4·044–4·126
Jan2	0·172–0·179	0·430–0·443	0·355–0·363	0·401–0·410	1·358–1·395
Total	1·315–1·363	6·757–6·946	12·673–12·953	10·398–10·662	31·142–31·925

Antarctica (Bester 1989; McConnell & Fedak 1996; Bornemann *et al.* 2000; van den Hoff *et al.* 2002). During the post-lactation phase, female southern elephant seals from Macquarie Island consumed an estimated 3478–3577 tonnes of fish within CCAMLR Statistical Subareas 88·1, 88·2 and 58·4·1 (Table 6). This is approximately 30 times greater than the mean annual commercial harvest of fish for this area between 1995–96 and 1998–99 (Table 8). In addition, they consumed 2·6 times more fish within the Australian/Macquarie Island EEZ than the mean annual commercial harvest between 1997–98 and 1998–99 (Table 8). Although fish are harvested commercially within these areas, squid have not been harvested in recent years (CCAMLR 2000; Goldsworthy *et al.* 2001). These data indicated that trophic interactions with commercial fisheries are minimal at present. Further, there is little opportunity for operational interactions. Future increases in fishing effort, however, may result in increased competition between the fishing industry and all top predators, including elephant seals. Alterations to the current trophic structure may also result.

One fishery, which may already compete with elephant seals, is that targeting toothfish (*Dissostichus* spp.). Catch limits for this genus of fish are currently set at 2508 tonnes for Subarea 88·1 and 250 tonnes for Subarea 88·2 (CCAMLR 2000). Although toothfish are currently believed to be a minor component of southern elephant seal diet (Slip 1995; I. Field, unpublished data) it is likely that future research on southern elephant seal diet will clarify this.

The model of energy and prey consumption used in this paper is simple. It is also subject to a number of assumptions, the first being that diving metabolic rate applies to all times of the foraging trip. The diving metabolic rate is lower than the field metabolic rate because it does not include the increased use of energy for the approximately 10% of the time that seals spend on the surface (Hindell & Lea 1998). The prey consumption values presented in this paper are therefore underestimates.

Additional bias is due to the poorly documented composition of southern elephant seal diet. Estimates are derived almost solely from small samples of stomach contents collected at the terrestrial haul-out sites (Rodhouse *et al.* 1992; Green & Burton 1993; Slip 1995; Daneri & Carlini 2002). These sites are, in most cases, thousands of kilometres from principal foraging

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Table 8. Mean commercial fishery catches (tonnes ± SE) from 1995–96 to 1998–99 for major cephalopod and fish taxa also eaten by southern elephant seals within fishery management zones: CCAMLR Statistical Subareas 58·4·1, 88·1 and 88·2 south of Australia (SAUS) and EEZ of Australia–Macquarie Island (MI-EEZ) and southern New Zealand (NZ-EEZ fisheries management area 6, FMA6) (CCAMLR 2000). Also shown are the mean estimated consumption values (tonnes) of fish and squid by breeding female southern elephant seals (SES) during the post-lactation (PL) period and annually (this study). For comparison, the corresponding catches within the South Georgia (SG) and Heard Island–MacDonald Island (HIMI) commercial fisheries zones within CCAMLR jurisdiction are also listed (CCAMLR 2000)

Taxon	CCAMLR-SAUS	MI-EEZ*	NZ-EEZ FMA6	CCAMLR-SG	CCAMLR-HIM
Squid					
Cephalopoda	0	0	4447 ± 145†	0	0
SES PL consumption	4969	1813	2267	NA	NA
Fish					
Channichthyida	< 0·5	0	NB	139 ± 133	95 ± 46
Macrouidae	16 ± 7	15	NB	18 ± 3	5 ± 4
Myctophidae	0	0	NB	5	0
Notothenidae	113 ± 93	551	NB	3441 ± 409	7131 ± 1337
Rajidae	12 ± 7	0	NB	25 ± 6	3 ± 1
Gadidae	0	0	31 933 ± 2534‡	0	0
Total mean fish	99 ± 81	566	31 933 ± 2534	3554 ± 458	7231 ± 1333
SES PL consumption	3528	1459	1824	NA	NA
Total mean fisheries	99 ± 81	566	18 190 ± 5367	3554 ± 458	7231 ± 1333
Total SES PL	8497	3272	4091	NA	NA
Total SES annual§	34 582	13 317	16 650	NA	NA

NA, data not available.
NB, negligible by-catch component, not targeted commercially.
*Mean annual catch from 1996–97 to 1998–99 (Goldsworthy *et al*. 2001).
†Mean commercial catch of arrow squid (*Nototodarus sloanii* and *Nototodarus gouldi*) from 1997–98 to 2000–01 (New Zealand Seafood Industry Council 2002).
‡Mean commercial catch of southern blue whiting *Micromesistius australis* from 1997–98 to 2000–01 (New Zealand Seafood Industry Council 2002).
§Assuming similar consumption rates over winter and a mean winter foraging trip duration of 237·3 days (C. Bradshaw & M. Hindell, unpublished data), the post-lactation trip represents a mean of 77·3/(77·3 + 237·3) = 0·2457 of the total time spent at sea per year. Annual values are therefore the post-lactation consumption multiplied by the reciprocal of 0·2457.

areas and most dietary remains are likely to have been voided by this time (Krockenberger & Bryden 1994). While the current estimates are an oversimplification (Boyd, Arnbom & Fedak 1994), they are the only ones available for use in trophic models. However, advances in diet-estimation technology, primarily through fatty acid signature analysis, will probably provide more information on which to base prey-consumption models (Best *et al*. 2003).

Conclusions

Even though they breed in the subantarctic, southern elephant seals from Macquarie Island spend a significant proportion of their time in Antarctic waters (*c*. 25% of total time in CCAMLR Statistical Subareas and in some months up to 36% of the population's time spent at sea in these Subareas). However, these figures represent the use and potential prey consumption for only one component of the population during only one season of the year. It is already known that male southern elephant seals spend more time in the high Antarctic during this time of year (Slip 1997a), and even adult females forage extensively in this region during winter (C. Bradshaw & M. Hindell, unpublished data). Recent work on juvenile seals from Macquarie Island also indicates that they too occupy significant portions of the subantarctic and Antarctic waters in this region (van den Hoff *et al*. 2002). At present, there have been too few juvenile and adult male seals, or adult females during winter, studied to apply the same kind of analysis to determine sample representativeness.

Elephant seals are likely to provide important information on the Antarctic marine ecosystem due to their tendency to forage within large regions of the CCAMLR management area. Large numbers of individuals suitable for study return to Macquarie Island each year, making them ideal candidates as monitoring organisms. This is particularly pertinent as preliminary data from longitudinal studies identify foraging site fidelity among years (C. Bradshaw & M. Hindell, unpublished data). However, southern elephant seals also forage in waters to the north of Macquarie, particularly during their dispersal phases. It is unlikely that the majority of their feeding occurs during these phases. Therefore, more data are required to assess the contribution of feeding during these times and the potential for conflict with commercial fisheries (Table 8; Goldsworthy *et al*. 2001). The data collected and analysed in this paper were part of a longer-term study of elephant seal foraging ecology in which winter foraging and diet composition data are at present being accumulated to provide eventually a clearer understanding of elephant seal consumption patterns within the Pacific sector of the Southern Ocean.

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