Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals

COREY J. A. BRADSHAW*, MARK A. HINDELL*, MICHAEL D. SUMNER*† & KELVIN J. MICHAEL†

*Antarctic Wildlife Research Unit, School of Zoology, University of Tasmania
†Antarctic Cooperative Research Centre & Institute of Antarctic and Southern Ocean Studies, University of Tasmania

Choices made by foraging animals should maximize energy intake, although 'irrational' short-term behaviours are common. One explanation for this is that environmental variation may lead to the evolution of behaviours that benefit individual reproductive output, but only over long timescales. Long-term (multiyear) fidelity to foraging regions in extremely variable environments may confer ecological benefits to individuals, such as familiarity with resources, even when energy gain is not consistently high in all years. We examined the annual foraging ranges (sometimes exceeding 3.5 million km^2) of female southern elephant seals, *Mirounga leonina*, over 4 years and found that individuals used preferred regions year after year. We hypothesized that the degree of fidelity in a particular year was related to the foraging success (as measured by mass gain) in the previous year; however, there was no significant relation between the two. Despite this high variation in annual foraging success, the regions revisited in consecutive years provided higher potential food production as measured by higher variance in sea surface temperatures over two decades (a surrogate measure of ocean productivity). The evolution of long-term fidelity assisted by simple navigational rules may confer energetic advantages over an individual's lifetime and explain the existence of seemingly nonadaptive short-term behaviours.

Foraging animals are expected to make judicious choices with respect to maximizing net energy gain (Stephens & Krebs 1986; Perry & Pianka 1997; Bateson 2002), but apparently 'irrational' behaviours (Bateson et al. 2002) are common (Stephens & Krebs 1986; Perry & Pianka 1997). Often additional information is required, especially with regard to the risk-sensitive trade-off between starvation and reproduction, before a sound understanding of the mechanisms underlying the evolution of foraging strategies is possible (Hurly 2003). One explanation for this is that environmental variation may lead to the evolution of

Correspondence and present address: C. J. A. Bradshaw, Key Centre for Tropical Wildlife Management, Charles Darwin University, Darwin, NT 0909, Australia (email: corey.bradshaw@cdu.edu.au). M. A. Hindell is at the Antarctic Wildlife Research Unit, School of Zoology, University of Tasmania, Private Bag 05, Hobart, Tasmania 7001, Australia. M. D. Sumner is at the Antarctic Wildlife Research Unit, School of Zoology, and the Antarctic Cooperative Research Centre & Institute of Antarctic and Southern Ocean Studies, University of Tasmania, Hobart, Tasmania 7001, Australia. K. J. Michael is at the Antarctic Cooperative Research Centre & Institute of Antarctic and Southern Ocean Studies, University of Tasmania, Private Bag 77, Hobart, Tasmania 7001, Australia.

behaviours that benefit individual reproductive output, but only over long timescales (Lewontin 1979; Bateson 2002). For example, long-term (multiyear) fidelity to foraging regions in variable environments may confer ecological benefits to individuals, such as familiarity with resources (Greenwood 1980), even when energy gain is not consistently high in all years. Many vertebrate species living in seasonally fluctuating environments demonstrate impressive migrations and long-term fidelity to foraging or breeding regions (Stewart & DeLong 1995; Block et al. 2001; Hamer et al. 2001; Lohmann et al. 2001). Although there has been some discussion of the ecological and evolutionary significance of returning to known foraging (nonbreeding) regions in insects (Beekman et al. 2003) and birds (Schmidt 2001), little information is available for mammals. For long-lived species, investigations of the evolutionary implications of foraging site fidelity are lacking, presumably because measuring lifetime reproductive output and longitudinal trends in body condition and individual foraging patterns is difficult (Perry & Pianka 1997).

An alternative approach is to examine the potential food availability over longer timescales by examining

variation in landscape structure (Peinetti et al. 2002). In the case of marine mammals that travel extensive distances from their breeding and haul-out sites to forage, the collection and analysis of remotely sensed time-series data of the oceanscape provides the means to examine the longer-term benefits of fidelity relative to potential feeding opportunity. The spatial distribution of biological resources in ocean ecosystems depends to some degree on the physical characteristics of the water column (e.g. temperature, salinity, water chemistry, currents, wind action, sea ice concentration, Denman & Abbott 1994; Loeb et al. 1997; Kögeler & Rey 1999; Rutherford et al. 1999). Indeed, the foraging patterns of marine organisms in higher trophic levels that depend directly or indirectly on the distribution and abundance of primary and first-order secondary production vary significantly with certain physical characteristics of the marine environment (Hindell et al. 1991a; McConnell & Fedak 1996; Guinet et al. 1997, 2001; Tynan 1997, 1998; Georges et al. 2000). Therefore, the measurement of long-term trends in physical characteristics of the ocean can sometimes provide a surrogate measure of temporal and spatial variation in food abundance when the appropriate spatial scales of investigation are chosen (Guinet et al. 2001; Fritz et al. 2003).

Elephant seals (*Mirounga* spp.) demonstrate some of the greatest horizontal and vertical movements of any mammal (Stewart & DeLong 1995); they have two migrations within the adult annual life cycle that can take them over 5000 km from their breeding sites (Stewart & DeLong 1995; Hindell & McMahon 2000; Hindell et al. 2003). Their capacity to return to the natal site to breed each year is well documented (Nicholls 1970). However, only preliminary data exist on the ability of individuals to navigate to and select specific oceanic habitats repeatedly during their foraging migrations. Previous observations of foraging site fidelity have been made for male and female northern elephant seals, *M. angustirostris* (Stewart & DeLong 1995; Le Boeuf et al. 2000), but the degree of spatial overlap in successive migrations has not been quantified, nor have the potential ecological or evolutionary implications of this observed spatial overlap been considered. We examined the marine foraging patterns of female southern elephant seals, *M. leonina*, over 4 years to identify the degree of fidelity to marine foraging areas. We hypothesized that variation in fidelity to foraging areas could be explained, in part, either by (1) short-term (annual) variation in foraging success (as measured by mass gain), or (2) longer-term variation in ocean productivity as measured by annual variation in sea surface temperatures. We discuss our results in terms of the potential mechanisms driving the evolution of this fidelity to foraging regions.

METHODS

Capture and Datalogger Deployment

Adult female southern elephant seals from Macquarie Island (54°30′S, 158°50′E) in the Pacific Sector of the Southern Ocean were captured, sedated, weighed (±1 kg) and equipped with Time–Depth Recorder archival tags (TDRs, Wildlife Computers, Redmond, WA, U.S.A., Bradshaw et al. 2002; Field et al. 2002) from 1999 to 2002 before their departure for the postlactation (PL, October–January) or postmoult (PM, February–September) foraging trip. All sampled females were of known age (born in 1993) to minimize the potentially confounding effects of age and cohort on the results (animals were marked previously for the purpose of another study, McMahon et al. 2003). Captures were done by hand where two researchers placed a canvas bag over the head of each animal and restrained it manually. Anaesthesia was achieved by administering an intravenous injection of tiletamine and zolazepam (Telazol; Fort Dodge, Iowa, U.S.A.) at a dose of 0.3–0.7 mg/kg in the extradural intravertebral vein (lumbar region) using a 90-mm 18G spinal needle (McMahon et al. 2000a). All efforts were made to minimize handling time and duration of anaesthesia. Sedation typically lasted 20–40 min depending on the individual, and recovery was defined as the time when the seal could raise its head and maintain it in the raised position (Slip & Woods 1996). Initial doses were given after the mass of an individual seal was estimated on the basis of previous experience by field personnel (Field et al. 2002). After sedation, seals were weighed to the nearest kilogram with a tripod, mesh net and electronic scales (Hindell & Slip 1997) so that precise mass-specific doses could be calculated. A seal was considered to be apnoeic when it had stopped breathing for longer than 5 min (Slip & Woods 1996). The seals' breathing and capillary refill of the gums were monitored constantly (Woods et al. 1994). An endotracheal tube, oxygen and the respiratory stimulant doxapram hydrochloride (Dopram, Fort Dodge, U.S.A.) were available in the event of prolonged apnoea or poor capillary refill, but were never required (McMahon et al. 2000a; Field et al. 2002). All animals recovered fully and were later observed behaving normally. All animal handling procedures were reviewed and approved by the Antarctic Science Advisory Committee.

The TDRs weighed around 400 g and so represented 0.10–0.16% of the departure mass of the adult female elephant seals in this study ($\overline{X} \pm SE = 320 \pm 6$ kg, range 246–401 kg; $N = 42$). They were attached to the dorsal surface of the seal between the shoulderblades by gluing them to the hair with a quick-setting epoxy (Araldite K268, Ciba-Geigy Corp., Basel, Switzerland, Hindell et al. 1991b). They were retrieved when the animals returned to shore by the same capture and sedation procedures described above. Retrieval of the TDR itself required carefully cutting the hair to which the TDR was glued (i.e. the skin remained intact). Once removed, the TDR's data were downloaded to a computer for processing. TDRs sampled time, depth, light level and temperature every 30 s for the duration of each foraging trip (Bradshaw et al. 2002). Daily locations were determined using geolocation by light levels (DeLong et al. 1992; Hill 1994) with Multitrace software (Jensen Software, Laboe, Germany). Daylength provides an estimate of latitude, and time of sunrise and sunset provides estimates of longitude, from standard equations for solar navigation (Yallop & Hohenkerk 1985; Nautical Almanac Office 1991).

Location Processing

Although satellite-linked tags provide more accurate at-sea positions than those derived by light levels, their acquisition can be costly (Bradshaw et al. 2002). Thus, in an effort to maximize sample size and the probability of obtaining repeat foraging trips, we opted to use the less precise but cheaper option of data-logging technology (TDRs, Bradshaw et al. 2002) to obtain at-sea locations. The resulting geolocations are subject to an error of at least 1 degree of latitude (Hill 1994) or more (Bradshaw et al. 2002) given the difficulty of estimating exact times of sunrise and sunset (Hill 1994). Uncertainty can arise from excessive travel by the animal between sunrise and sunset, excessive crepuscular diving activity, atmospheric aberration and daylength ambiguity at equinox periods (Hill 1994). Therefore, to process locations, we used a Kalman filter developed to smooth the geolocation-estimated trajectories of marine vertebrates (Sibert et al. 2003). Once filtered, the tracks for each seal and for each foraging trip were summarized by time per unit area to incorporate the remaining uncertainty in foraging trajectories. This was done by creating a raster latitude/longitude grid with cells of 300×300 km. The spatial scale was determined by maximizing the agreement between TDR-recorded temperatures and satellite sea surface temperature data (Vazquez et al. 1998) based on previous methodology (Bradshaw et al. 2002) and estimating the time spent per cell by each individual. For this we used a series of computational routines developed in Interactive Data Language (IDL 5.0, Research Systems Inc., Boulder, Colorado, U.S.A.) that calculated the total time spent by an individual seal within each of the defined grid cells centred on the track (Bradshaw et al. 2002). The time-spent value assumed a constant rate of travel between successive locations.

We also determined the maximum distance travelled from Macquarie Island for each individual foraging trip by calculating the distance (d) between the centre of the grid cell furthest from Macquarie Island using the great circle distance formula:

$$d = \arccos(\sin y_1 \sin y_2) + \cos y_1 \cos y_2 \cos(x_1 - x_2) \quad (1)$$

where y_1 = longitude of Macquarie Island, x_1 = latitude of Macquarie Island, y_2 = longitude of the furthest point and x_2 = latitude of the furthest point. The compass bearing (b) to this furthest point for each individual was calculated as:

$$b = 2\pi - \mathrm{mod}\big[\arctan(\cos y_1 \sin y_2 \\ - \sin y_1 \cos y_2 \cos(x_1 - x_2), \sin(x_1 - x_2)\cos y_2), 2\pi\big] \quad (2)$$

where b is in radians, 'arctan' = arctangent of the first and second terms (in radians) between $-\pi$ and π, excluding $-\pi$ and 'mod' signifies the remainder of the solution in the arctangent equation divided by 2π.

Statistical Analyses

We calculated the overlap between successive foraging trips by estimating the proportion of grid cells in common from year i to year $i + 1$ relative to all grid cells. We also examined whether the distribution of spatial overlap was also borne out by the distribution of time spent per grid cell. For this, grid cells in common from year i to year $i + 1$ were compared using randomized linear regression (20 000 iterations, Manly 1997) on the proportion of time spent per cell. We estimated regional use on a finer scale by comparing the proportion of time spent per 300- $\times$ 300-km grid cell between consecutive trips. We analysed only those grid cells for which there was use in the consecutive year's foraging trip (i.e. removed all zero values) using randomized linear regression and a generalized linear model of the form:

$$\mathrm{arcsine}\sqrt{\mathrm{proportion\ time\ spent}_i} \\ = \mathrm{arcsine}\sqrt{\mathrm{proportion\ time\ spent}_{i+1}} + \mathrm{individual} \quad (3)$$

where i = year.

The high degree of individual overlap of foraging regions in consecutive years (see Results) led us to pose hypotheses on the potential benefits of fidelity in terms of foraging success. Elephant seals acquire large quantities of energy during their biannual foraging trips and store this mainly in the form of blubber (Fedak et al. 1994). Examining this relative mass gain (mass gain/departure mass) for an individual compared to her degree of fidelity allowed us to test the hypothesis that the mass gain in year i could be used as a predictor of overlap in year $i + 1$. This relation may exist because successful individuals may be familiar with the location of relatively more productive regions than their less successful conspecifics (Schmidt 2001). Mass gain relative to area overlap and area traversed was compared using randomized linear regression.

To investigate the potential longer-term productivity of oceanic foraging regions, we examined the temporal (annual) variation in sea surface temperatures (SSTs) within the foraging range of elephant seals from Macquarie Island using the Pathfinder SST monthly data sets (Version 4.1; best SST; 18-km spatial resolution; ascending pass) derived from the multichannel Advanced Very High Resolution Radiometer (AVHRR), NASA Physical Oceanography Distributed Active Archive Center (Vazquez et al. 1998). We used all the available Pathfinder data sets (1985–2002) and calculated the standard deviation (SD) of SST per pixel over the 18–year period to construct a temporal 'climatology' (i.e. an assessment of the temporal patterns of variability over a long period, Sumner et al. 2003). Temporal SD of SST per pixel also provides information on the spatial variability in SST because, although there is some degree of predictability in the position of fronts (Budillon & Rintoul 2003), their positions do vary between years (Sokolov & Rintoul 2002). Therefore, pixels within the vicinity of frontal zones will demonstrate larger SD of SST over time. Within the middle of each foraging trip (PL: November–December; PM: June–August) we constructed monthly grids per seal and determined the degree of spatial overlap between years for each individual. The resulting grids were classed as 'overlapping' or 'not overlapping' between years accordingly. Only those seals for which there was at least one grid cell overlapping were used in the PM months (all

PL seals had overlapping cells in November–December). The Pathfinder SST SDs for each month were overlaid on to each seal's gridded monthly distribution. We removed all pixels for which there were <2 years of data for the estimation of annual SST SD. The distributions of SST SDs within and outside the regions of annual overlap for each seal were pooled per month and compared using a Monte Carlo approach. Owing to different numbers of pixels within and outside the regions of overlap, we sampled 100 SD values from each region, calculated the mean SD, and repeated this procedure 10 000 times to produce comparable distributions. We also compared the mean SD for within and outside of overlapping regions using 10 000 randomizations.

We also summarized the percentage of time spent by all sampled seals within the vicinity of the major frontal zones of the Southern Ocean: (1) the Subantarctic Front (SAF); (2) the Antarctic Polar Front (APF); and (3) the southern boundary of the Antarctic Circumpolar Current (SACC). The limits of these frontal zones were defined as the average position of the fronts compiled from all historical hydrographic stations collected before and including 1990 (Orsi et al. 1995). A grid cell was deemed to be in the vicinity of each particular frontal zone when the average position of the front passed through the grid cell. On a few occasions, more than one front passed through the same grid cell. In these situations we allocated the grid cell to the front that passed closest to the centre of the grid cell.

RESULTS

Maximum Distance and Bearing

We collected data on repeat foraging trips from 19 adult female southern elephant seals from Macquarie Island ($N = 26$ individual foraging trips). For eight individuals, successive summer (PL) foraging trips were available (PL 1999 to PL 2000; $N = 8$ trip pairs; Fig. 1), and for 11 individuals at least two winter (PM) foraging trips were available (PM 1999, 2000, 2001, 2002; $N = 15$ trip pairs; Fig. 2). Among individuals, the mean ± SE maximum distance travelled from Macquarie Island was 1392 ± 157 km for PL (range 644–2555 km) and 2747 ± 131 km for PM (range 1483–3844 km). Maximum distance travelled by an individual in year i was a good predictor of her maximum distance travelled in year $i + 1$ for both seasons (all adjusted $r^2 \geq 0.69$; Fig. 3a). The mean ± SE azimuthal bearing from Macquarie Island to the maximum distance location was 188.5 ± 18.0° for PL (range 113–316°) and 161.5 ± 9.2° for PM (range 100–264°) and again the bearing travelled by an individual in year i was a good predictor of her bearing in year $i + 1$ (all adjusted $r^2 \geq 0.82$; Fig. 3b).
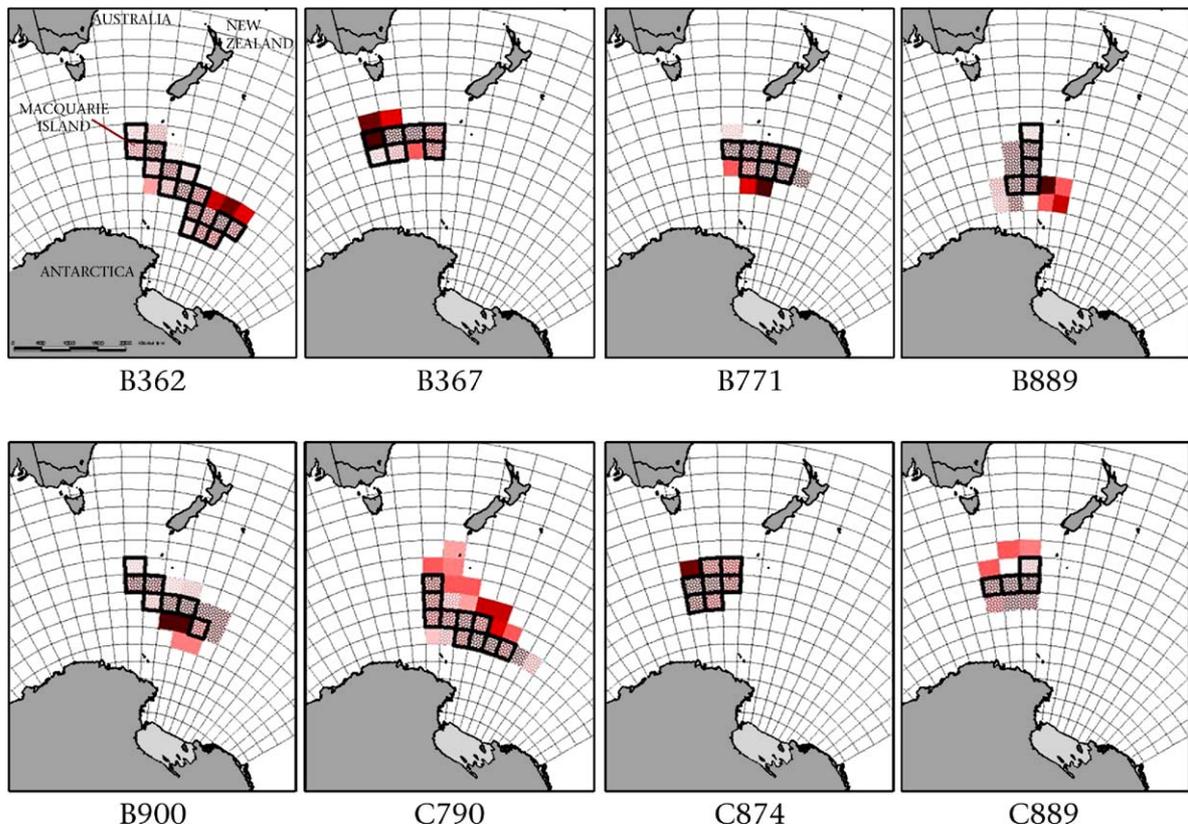
Figure 1. Foraging regions of eight female southern elephant seals during the postlactation (October–January) foraging trips in 1999 (solid squares) and 2000 (dotted squares). Regions of overlap between years are outlined in black. Darker cell colours indicate more relative time spent in those grid cells.
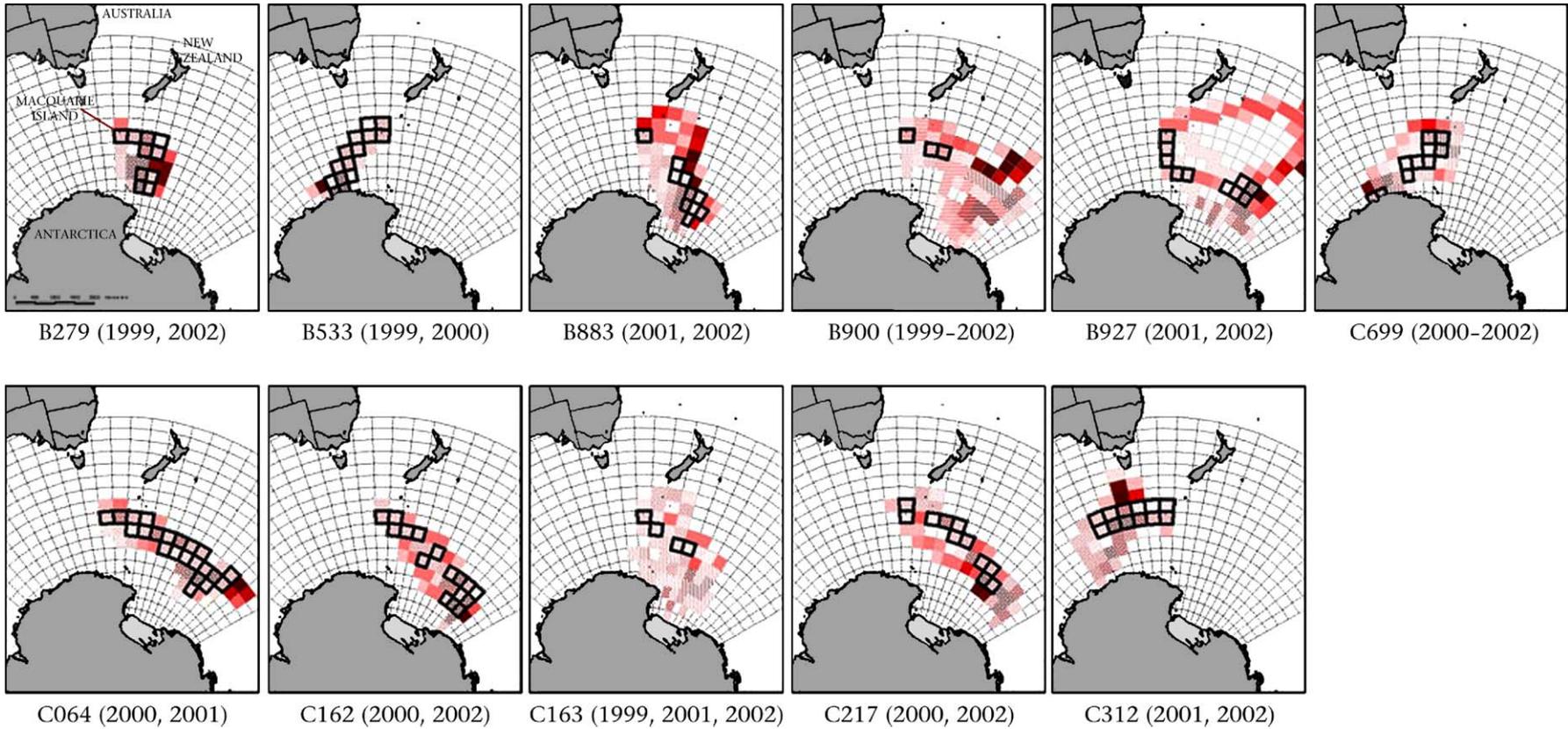
Figure 2. Foraging regions of 11 female southern elephant seals during the postmoult (February–September) foraging trips between 1999 and 2002. Regions of overlap between years are outlined in black. Note for B900, C163 and C699, overlap regions were common to more than 2 years. Darker cell colours indicate more relative time spent in those grid cells.
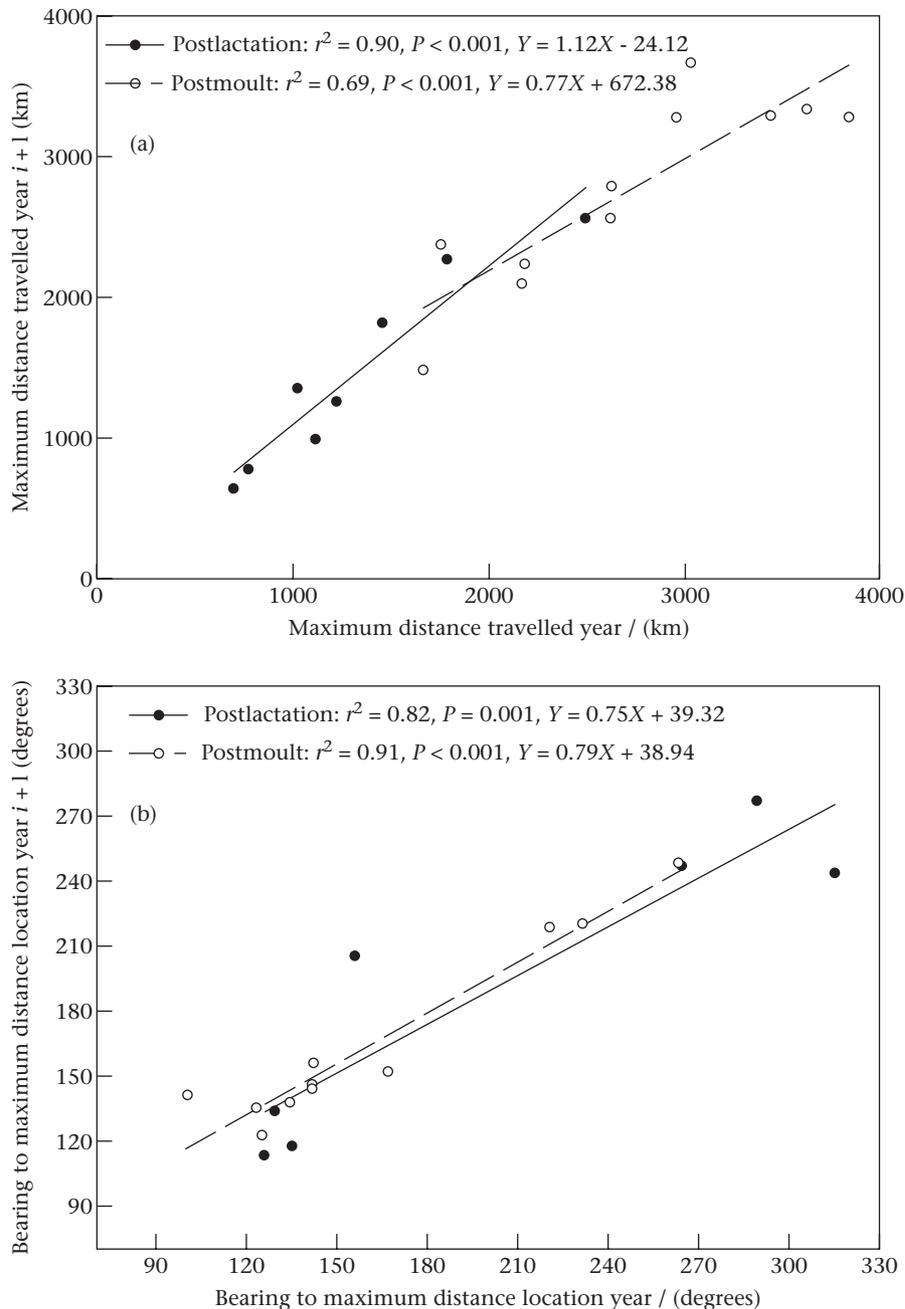
Figure 3. (a) Relation between the maximum distance travelled from Macquarie Island by an individual in year $i + 1$ to that travelled in year i for both the postlactation and postmoult foraging trips. (b) Relation between the azimuthal bearing to the maximum distance location in year $i + 1$ to the bearing travelled in year i for both the postlactation and postmoult foraging trips.

To determine whether foraging routes were unique to individual seals, we also compared the maximum distance and bearing of trip pairs (trips i and $i + 1$) with those from a sample of adult females tracked only in year $i + 1$ ($N = 3$ PL and $N = 11$ PM additional individuals). Randomized linear regression showed that maximum distance was unique for trip pairs in all years ($P_{20\,000} < 0.04$) except PM 2000 for which there were only two pairs ($P_{20\,000} = 0.10$). Similarly, trip bearing was unique for all PL and PM trips for all years ($P_{20\,000} \leq 0.02$). This result excludes the possibility that individual fidelity

was due to all individuals moving to the same general area of the Southern Ocean and it demonstrates that individual fidelity to foraging region was nonrandom.

Foraging Area Overlap

Individual foraging areas overlapped a mean $\pm$ SE of $65.7 \pm 5.1\%$ ($N = 8$ trip pairs; range 48.1–86.8%; Fig. 1) between successive PL foraging trips. For PM foraging trips, the area overlap between successive years was
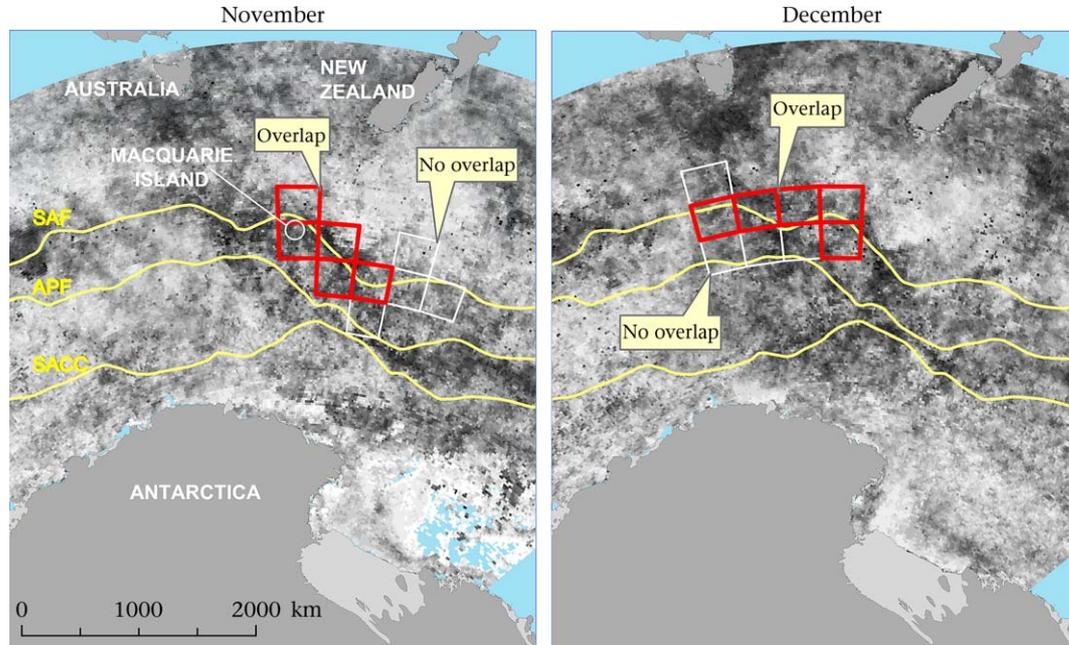
Figure 4. Pathfinder sea surface temperature (SST) temporal standard deviation (SD) for 1985–2001 for the focal postlactation months of November and December. Darker shades indicate higher SD values. Also shown is an example of the overlapping and nonoverlapping regions for individuals B900 (November) and B367 (December). The average limits of the Subantarctic Front (SAF), Antarctic Polar Front (APF) and the southern boundary of the Antarctic Circumpolar Current (SACC) are shown (from Orsi et al. 1995).

54.3 $\pm$ 6.2% ($N = 11$ trip pairs; range 19.3–88.8%; Fig. 2). Including all trip pairs (i.e. with nonsuccessive trips), PM area overlap was 53.3 $\pm$ 4.6% ($N = 15$; range 19.3–88.8%; Fig. 2). Not only did individuals visit the same general regions year after year, but the proportion of time spent in finer-scale regions (300 × 300-km cells) in one year also explained a significant proportion of the variation in the time spent in those regions the following year. On pooling individuals, we found a weak positive correlation for the proportion of time spent in grid cells between consecutive years for the PL trips ($r^2 = 0.20$, $P_{20\,000} < 0.001$) and for the PM trips ($r^2 = 0.13$, $P_{20\,000} < 0.001$). The model examining the relation by individual identified a significant relation between consecutive trips for both seasons (PL: $F_{1,53} = 11.08$, $P = 0.002$; PM: $F_{1,217} = 21.96$, $P < 0.001$), but there was no evidence for a difference between individuals (PL: $F_{7,53} = 0.71$, $P = 0.67$; PM: $F_{10,148} = 0.85$, $P = 0.59$).
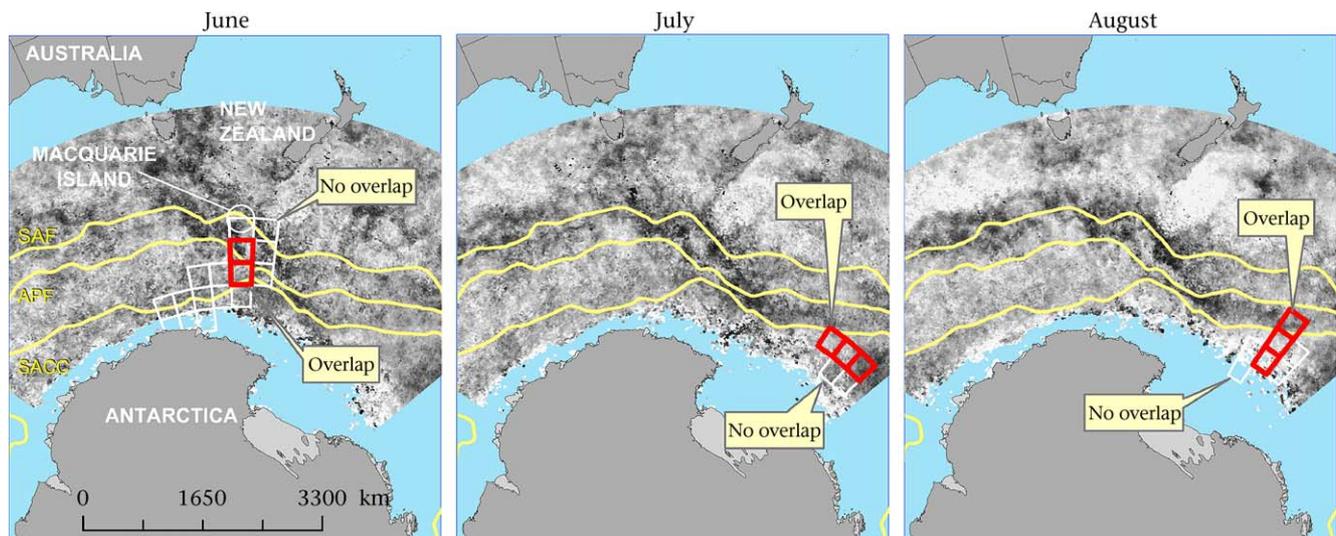
Figure 5. Pathfinder sea surface temperature (SST) temporal standard deviation (SD) for 1985–2001 for the focal postmoult months of June–August. Darker shades indicate higher SD values. Also shown is an example of the overlapping and nonoverlapping regions for individuals C699 (June), C162 (July) and C064 (August). The average limits of the Subantarctic Front (SAF), Antarctic Polar Front (APF) and the southern boundary of the Antarctic Circumpolar Current (SACC) are shown (from Orsi et al. 1995).

Table 1. Mean standard deviation (SD) of annual Pathfinder sea surface temperature (SST) per foraging trip and per month within and outside the regions of spatial overlap in spatial grid cells and the randomization rejection probabilities for the difference in mean SD between overlapping and nonoverlapping regions

| Foraging trip month | Mean Pathfinder SST SD | | |
	Outside region of overlap*	Within region of overlap*	P†
Postlactation			
November	0.7645	0.8144	<0.0001
December	0.8088	0.8289	<0.0001
Postmoult			
June	0.6543	0.7011	<0.0001
July	0.7097	0.7251	0.0002
August	0.6117	0.6535	<0.0001

*10 000 samples of 100 pixels.
†10 000 randomizations of mean Pathfinder SD.

Mass Gain

Relative mass gain (RMG) of individual seals with consecutive foraging trips was highly variable. Mean female RMG ± SE was 36.7 ± 3.0% (years combined) during the PL trip, and 66.6 ± 3.0% (years combined) during the PM trip. The change in RMG ($RMG_i - RMG_{i+1}/RMG_i$) between years for individuals was −51.2–68.1% for PL trips and −24.9–69.6% for PM trips. Thus, seals returned to the same regions and remained there, even when they did relatively poorly in a previous year. There was no evidence to reject the null hypothesis ($P_{20\,000} = 0.36$): mass gain was not a good predictor of spatial overlap. We also hypothesized that less successful individuals might increase the area they traverse in search of more profitable areas if they demonstrate the ability to compensate for poor foraging conditions in a particular year. However, there was no relation between the maximum area traversed and the relative mass gain per

Table 2. The percentage total time spent by adult female elephant seals in the vicinity of the average positions (Orsi et al. 1995) of the three main frontal zones within the Pacific Sector of the Southern Ocean: (1) the Subantarctic Front (SAF); (2) the Antarctic Polar Front (APF); and (3) the southern boundary of the Antarctic Circumpolar Current (SACC) as well as outside of these frontal zones (FZ)

| Foraging trip month | Percentage of time | | | |
	Around SAF	Around APF	Around SACC	Outside FZ
Postlactation				
November	40.1	14.8	16.0	29.1
December	27.0	31.4	13.8	27.8
Postmoult				
June	22.3	16.5	25.7	35.5
July	26.3	4.3	27.5	41.9
August	12.8	10.9	36.1	40.3

All percentages are summarized by month for the focal foraging period of each annual foraging trip (postlactation and postmoult).

individual for either the PL trip ($N = 14$ trips, $P_{20\,000} = 0.52$) or the PM trip ($N = 25$ trips, $P_{20\,000} = 0.14$). This result also suggests that there were no additional costs to travelling further for the most wide-ranging females.

Sea Temperatures and Time in Frontal Zones

Therefore, fidelity to a particular region may not necessarily provide short-term (i.e. year-to-year) benefits because seasonal variation in ocean productivity is high (Constable et al. 2003). However, fidelity to regions that show higher productivity on average over the lifetime of an individual female seal (up to 24 years) may maximize the net energy gain over the longer term (i.e. decades). We examined the annual variability (1985–2001) in monthly sea surface temperatures (SST) over the entire foraging range of Macquarie Island elephant seals. We predicted that focal foraging regions would show higher variance in SST over the interval of a female elephant seal's life span because temporal and geographical variation in SST can be used as a surrogate for regional marine productivity (e.g. higher temperature gradients across frontal zones, Rutherford et al. 1999; van Franeker et al. 2002). Without exception, the SDs of SST were higher in the regions of annual overlap than in those regions falling outside the overlapping grid cells for each seal in each month examined in both the PL (Fig. 4) and PM foraging trips (Fig. 5, Table 1). Although the differences between overlapping and nonoverlapping cells appeared small, the large number of pixels examined and the long time series will necessarily result in small variance values over a spatial grain of 300 × 300 km. Therefore, the consistency of the differences between all seasons and individuals examined shows a biologically meaningful result.

Table 2 shows the percentage of time that seals spent within the vicinity of each major frontal zone. During the PL trip seals spent most of their time around the SAF in November, but moved towards the APF during December. This result is consistent with previous spatial summaries of adult female use during this period (Hindell et al. 2003). During the PM trip, however, most time was spent within the vicinity of the SACC and outside the frontal zones when seals were generally moving much further south during the longer winter foraging trip.

DISCUSSION

The capacity for wide-ranging animals to navigate to and from their breeding and foraging regions has generated much interest, but largely in terms of the navigation mechanisms used (Hays et al. 2003; Wehner 2003). The evolutionary significance of fidelity has received considerably less attention. When habitats vary temporally and spatially in composition, and individuals cannot immediately or accurately assess habitat quality, then experience (e.g. reproductive output, body condition) may be used as a surrogate measure (Schmidt 2001). In the case of nonbreeding ranges, fidelity should be determined by ecological factors and not by factors related to mate selection (Sandercock & Jaramillo 2002). Individuals

might therefore show higher fidelity if more successful during previous foraging trips. This rule, known as the win-stay/lose-switch rule (Shields et al. 1988), did not apply to shorter-term foraging success of elephant seals as measured by weight gain. The lack of an obvious foraging advantage with increased feeding area specialization in the short term has also been reported for Adélie penguin, *Pygoscelis adeliae*, feeding frequency (Watanuki et al. 2003). Our results showed that, although there may be no shorter-term advantage of fidelity as measured by weight gain (indeed, there may be an immediate disadvantage for that year's reproductive output, McMahon et al. 2000b), this behaviour may serve to maximize net energy gain over an animal's lifetime (Perry & Pianka 1997; Schmidt 2001). Although our results are tantalizing, the lack of data on longer-term survival and lifetime reproductive output from the sampled females prevents a definitive conclusion regarding long-term benefits of fidelity in this species.

None the less, the selective pressure of maximizing lifetime energy intake should eventually lead to the evolution of long-term fidelity to regions with higher average productivity in long-lived, wide-ranging species occupying variable environments, even if these regions are sometimes not as profitable. Although there is some spatial predictability in the structure of the major frontal zones within this region of the Southern Ocean (Budillon & Rintoul 2003), the latitudes of the fronts themselves vary between years and are correlated with variation in sea surface temperatures (Sokolov & Rintoul 2002). Higher temperature gradients within frontal systems generally indicate higher relative productivity than surrounding areas (Rintoul et al. 2001; Moore & Abbott 2002), so these features are potentially important for vertebrate marine species originating from Macquarie Island (Hull 1999a, b; Field et al. 2001; Hindell et al. 2003). The high percentage of time spent within the vicinity of the SAF and APF during the postlactation foraging trip supports this conclusion. Although it can be argued that some degree of spatial predictability in the frontal structure exists for this region, the diversity of foraging areas among individuals (i.e. individuals were not all targeting specific areas) suggests that individual specialization over the longer term is a more important behavioural adaptation to variable food resources than compensatory movement to different foraging regions. Seals spent a relatively lower proportion of time within the vicinity of frontal zones during winter as they moved south towards the Antarctic continent, which lends support to the idea that frontal features are not necessarily the driving force behind the selection of individual foraging regions.

This hypothesis implies that, at least at the coarse, regional scale of multiannual foraging patterns, decisions are not made by the individual to compensate for localized prey depletions; rather, the selective advantage of developing fidelity early in life may result from the higher probability of sequestering appropriate food stores for maintenance and reproduction after learning successful foraging routes as juveniles (McConnell et al. 2002). The development of the fidelity behaviour itself may be the product of initial success (survival) during the juvenile years, resulting from a combination of having sufficient body reserves postweaning (McMahon et al. 2000b) and random events, leading to an increased probability of juvenile survival in unfamiliar habitats during the first few trips to sea (McConnell et al. 2002). We emphasize that our results were derived from already successful adults benefiting from 6 or more years of foraging experience. The ability of southern elephant seals to modify foraging patterns in response to smaller patches of prey encountered while transiting to preferred individual regions remains to be tested at finer spatial scales (i.e. using satellite technology) (Fritz et al. 2003).

The strong relations between the maximum distance travelled and the main trip bearing from year to year suggest that elephant seals may use simple rules (use a bearing corrected for current drift and travel a maximum distance within a set time) to assist their navigation to individual foraging areas despite the high variability in the physical configuration of the ocean (e.g. currents). It is likely, however, that elephant seals also use finer-scale navigational cues from their environment to adjust their foraging routes (Stern 2002). Experiments with juvenile marine turtles, *Caretta caretta*, indicate that geomagnetic cues may be responsible for at least some of the precision of navigation in the open ocean (Lohmann & Lohmann 1998). However, in some areas of the ocean, the use of bicoordinate magnetic navigation is improbable (Åkesson et al. 2001). It has been suggested that visual cues, wave direction and windborne and current cues may all contribute to navigation in marine turtles (Papi et al. 2000; Åkesson et al. 2001; Hays et al. 2003). In the case of elephant seals that migrate to particular pelagic foraging areas, visual cues are not possible because of the seals' inability to dive to the ocean floor and the absence of land as points of reference. However, currents and eddies associated with frontal zones, temperature gradients, low-frequency sound transmission, wind patterns and even chemosensitivity may all contribute to the seals' navigation (McConnell et al. 2002).

The choice of scale used to estimate overlap will, to some extent, dictate the results of intraindividual overlap. For example, an overly coarse spatial scale would result in high overlap between years, but a fine scale might not result in any overlap. However, the variation in interindividual use was greater than that of intraindividual use of the ocean environment, suggesting that our conclusions are robust to the choice of spatial scale. Furthermore, the 300-km scale represented an average of only 23% (PL) and 12% (PM) of the maximum distance achieved from Macquarie Island. Thus, although the fine-scale components of the foraging trip were not assessable, the general geographical patterns were discernible for the purposes of determining regional fidelity.

In conclusion, our results reveal a possible mechanism whereby wide-ranging predators can 'predict' a suitable foraging range, at least at the spatial scale examined here, in an environment where the distribution of food resources is highly variable in time and space. We suggest that much of seal navigation to individually preferred foraging regions is achieved, at least partially, through the

sequence of initial success followed by simple rules of repeat bearing and maximum distance. Furthermore, we propose that this mechanism leads to the evolution of individual niche specialization, a process now thought to have profound effects on the ecological and evolutionary dynamics of populations (Bolnick et al. 2003). Finally, we suggest that the development of long-term fidelity to oceanic foraging regions and individual diet specialization (Bradshaw et al. 2003) might confer a lifetime energetic advantage where individuals remain faithful to regions of potentially higher productivity within an extensive and highly variable environment.

Acknowledgments

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