



Climate-scale hydrographic features related to foraging success in a capital breeder, the northern elephant seal *Mirounga angustirostris*

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ABSTRACT: In marine ecosystems, physical and biological processes act at multiple temporal and spatial scales to influence the distribution of prey species and subsequently habitat selection of foraging apex predators. Understanding how apex predators may respond to climate changes requires knowledge of habitat selection in relation to measures of foraging success at spatio-temporal scales relevant to the question and analytical approach. In this study, we used satellite telemetry from 75 adult female northern elephant seals *Mirounga angustirostris*, coupled with point measures of foraging success (energy gain), to examine habitat selection at large temporal and spatial scales. The main hydrographic ecoregion used on the post-moult (PM) migration was the Transition Zone, while on the post-breeding (PB) migration, females focused on the Subarctic Gyre. Characteristics of area-restricted search (ARS) behaviours, as determined by the fractal landscape method (such as time spent in ARS, total distance travelled in ARS and number of ARS) also differed significantly between the PM and PB migrations. Underlying differences in prey composition and/or distribution may drive the differences seen in searching behaviour and foraging success of elephant seals at large scales. Despite these differences, seals showed comparable levels of foraging success across both migrations and in all ecoregions. Foraging success was notably greater than measured in previous studies. These results highlight the benefits of a capital breeding strategy to a relatively slow-moving, large vertebrate predator allowing individuals to exploit large areas of the heterogeneous North Pacific.

KEY WORDS: Apex predator · North Pacific · Transition Zone · Subarctic Gyre · Habitat selection

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INTRODUCTION

In marine systems, the importance of scale has long been recognised, with processes shaping the environment acting at several temporal and spatial scales (Steele 1988, Mann & Lazier 1996). Aggregations of species also occur at different temporal and spatial scales relating to different environmental effects, from the aggregation of

zooplankton at the thermocline (Russell et al. 1999) to aggregations of fishes, squid and other vertebrate predators within frontal systems (Lefevre 1986, Russell et al. 1999, Field et al. 2001, Polovina et al. 2001). Fronts have been shown to delineate species distributions (Brinton 1962, Beamish et al. 1999, Sassa et al. 2002), although the specific mechanisms responsible often require careful investigation (Sournia 1994).

Three climate-scale hydrographic zones, or eco-regions, persist in the North Pacific (Fig. 1a). However, their seasonal locations vary (Fig. 1b), and at the boundaries between zones several fronts may occur at any time with mesoscale eddies and submesoscale jets contributing to complexity and creating patches of productive areas a few km across (Roden 1991). The 3 eco-regions and their 2 frontal boundary regions constitute 5 latitudinal zones of the North Pacific (Roden 1991) that have been shown to delineate species distributions of zooplankton (Brinton 1962) and fishes (Beamish et al. 1999, Sassa et al. 2002) and are of ecological importance to some apex predators (Polovina et al. 2000, Hyrenbach et al. 2002). One particular frontal system that has received a lot of attention is the Transition Zone Chlorophyll Front (TZCF, operationally defined at 0.2 mg m^{-3}), which has been associated with

movement patterns of turtles and the distribution of albacore tuna (Polovina et al. 2001). The TZCF moves up to 1000 km in latitude annually but is usually contained within the climatological mean position of the Transition Zone (Roden 1991, Polovina et al. 2001, Bograd et al. 2004).

Although productivity increases with latitude in the North Pacific at macro scales, the mesoscale eddies shed in the frontal zones act to locally enhance productivity from intermediate temporal (weeks) and spatial scales (100s km), down to a few km (Roden 1991). To find food in a patchy environment such as this, animals utilise area-restricted search (ARS) patterns at various scales (Bell 1991). ARS patterns maximise the localisation of prey and time spent in areas with abundant resources and extend the search to larger areas when resources become scarce (Bell 1991, Hills et al. 2004).

ARS behaviour is affected by the mobility of the animal, the distribution and quality of resources, and the physiological need of the animal (Bell 1991). Foraging success can be considered as maximisation of energy gain relative to time or energy spent searching for food. Within a patchy hierarchical system, such as the North Pacific, we expect to find different behavioural patterns at different operational scales (Bell 1991, Guinet et al. 2001, Hyrenbach et al. 2002). These patterns will be influenced by characteristics of the patch. For example, given a high density of high quality resources within a patch, we might expect an individual to spend more time searching in, or more effort to return to, this patch than a patch with lower density or quality of resources. By linking searching behaviour to measures of foraging success, such as mass or energy gain, we can ascertain the ecological significance of selected habitat and better understand potential impacts of climate change.

With the increased use of electronic instruments to remotely track large or wide-ranging animals, movement patterns and foraging behaviour can now be examined on global and multi-year time scales (Polovina et al. 2004, Block et al. 2005, Shaffer et al. 2006, Weng et al. 2008). Tracking characteristics such as turn angle, transit rate, and first passage time or fractal dimension have been used to examine the movement patterns of multiple marine species

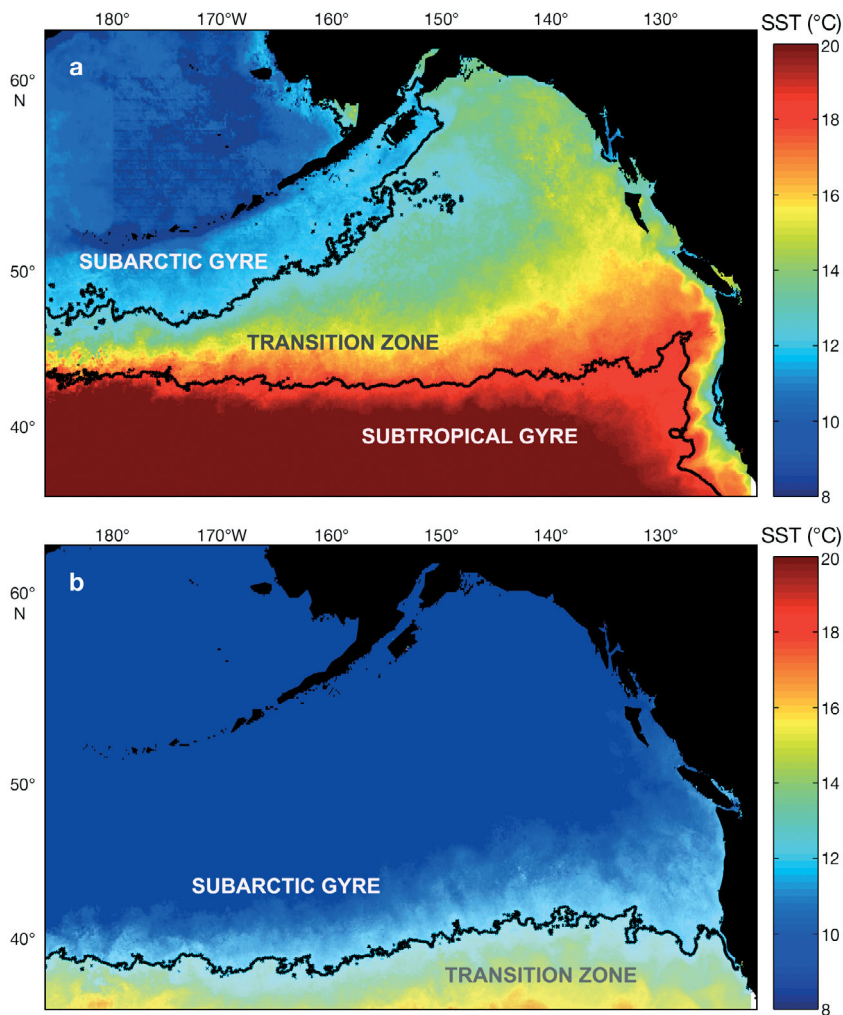


Fig. 1. Blended monthly 0.1° sea surface temperature (SST) for (a) September 2005 and (b) April 2005. Data courtesy of NOAA's Environmental Research Division (<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp>). Contours drawn at 12°C and 18°C delineate climate-scale hydrographic features following Longhurst (1998) and Weng et al. (2008)

(Weimerskirch et al. 1994, Laidre et al. 2004, Robinson et al. 2007). These approaches are often used as a proxy for feeding success to identify areas important to foraging animals. Characterisation of the environment in these areas is therefore vital to understand which cues animals use to find food, and/or what features might be contributing to increased productivity. Both remotely sensed data (Polovina et al. 2000, Simmons et al. 2007) and *in situ* data from instruments carried by the animals themselves can be used to characterise their immediate environment (Hindell et al. 1991a, Lydersen et al. 2002). This information could then be used to model an animal's response to changes in its environment.

Northern elephant seals *Mirounga angustirostris* offer a unique opportunity to examine how an apex predator searches a complex environment for prey, as they spend up to 10 mo of the year ranging widely across the North Pacific, while continuously probing its subsurface structure to depths of 400 to 600 m every 20 min, on average (Le Boeuf et al. 1986, 1988, 2000). A female elephant seal's annual cycle is divided into 2 distinct periods of resource acquisition at sea and 2 periods of resource allocation on land for breeding and moulting. As capital breeders (Jönsson 1997), all of the resources that females allocate to reproduction are acquired during a single foraging trip (or post-moult [PM] migration) lasting up to 8 mo prior to breeding. Thus, foraging success on this migration has a direct influence on reproductive success as well as the condition of individual females.

Previous studies have identified areas of 'focal foraging effort' for elephant seals, based on a reduction in the mean daily transit rate, that were coincident with an increase in foraging-type dives as well as mass gain (a measure of foraging success) while at sea (Le Boeuf et al. 1988, 2000, Crocker et al. 2006) and considered these areas in relation to satellite-derived oceanographic features (Simmons et al. 2007). Adult females behave optimally with regard to time spent within a foraging patch versus travel time to that patch (Charnov 1976, Crocker et al. 2006). However, this relationship broke down during the 1997/98 El Niño and was accompanied by a significant decrease in mass gain, although animals still visited similar regions of the North Pacific (Crocker et al. 2006).

Crocker et al. (2006) suggested that El Niño conditions may alter the hydrography that helps determine prey patch characteristics, and thus females may respond to inappropriate oceanographic cues while searching for prey. The goals of our study were to examine searching behaviour and foraging success of adult female northern elephant seals relative to climate or macroscale hydrographic features of the North Pacific. We hypothesised that (1) searching behaviour

(characteristics of ARS) will vary by ecoregion used, indicative of different prey species/distributions in each ecoregion; (2) female elephant seals will use different hydrographic ecoregions on their 2 annual foraging migrations; and (3) foraging success will vary, with higher rates of energy gain associated with more productive, higher latitude ecoregions.

MATERIALS AND METHODS

To examine the searching behaviour of adult female northern elephant seals, we used satellite transmitters to obtain at-sea locations from 75 migrations. Satellite and VHF transmitters were deployed from a colony at Año Nuevo State Reserve (San Mateo County, California, USA). Females were instrumented in April to June after the moult and transmitters were recovered in January to February (PM migrations; 2004: $n = 19$, 2005: $n = 19$). Females were also instrumented in February to March following the breeding season and transmitters were recovered in April to May (post-breeding [PB] migrations; 2005: $n = 18$, 2006: $n = 19$).

Satellite transmitters used included Telonics ST-20 ($n = 2$), Wildlife Computers Spot4 ($n = 52$), and Sea Mammal Research Unit, Satellite Relay Data Loggers (SRDLs, $n = 21$). Each female was also equipped with a VHF radio tag (ATS) that allowed individual animals to be relocated upon return to the colony.

Animal handling. The seals were initially sedated using an intra-muscular injection of Telazol[®] at an estimated dose of 1 mg kg^{-1} , and sedation was maintained with intravenous doses of ketamine and valium as necessary (Briggs et al. 1975, Baker et al. 1990).

Satellite transmitters were attached to the head of the seal using a quick-setting 5 min epoxy (Loctite[®] Quick Set[™] Epoxy). Radio transmitters were attached on a single nylon mesh patch to the dorsal midline just posterior to the shoulder blades. While the females were sedated, blubber depth measurements were taken at 6 points on the dorsal, lateral and ventral sides using an ultrasound scanner accurate to $\pm 1 \text{ mm}$ (Scanoprobe). Length and girth measurements were also taken at these points and used in a model of truncated cones to calculate total blubber mass as a percentage of body mass (Gales & Burton 1987, Webb et al. 1998). Females were rolled onto a canvas sling, suspended from a carbon fibre tripod using a come-along and weighed using a Dyna-Link scale ($1000 \pm 1 \text{ kg}$, Measurement Systems International).

Instruments were recovered when the females returned to the colony. Ultrasound, morphometrics and mass measurements were also collected at this time. For the PB migration, instruments were recovered as soon as possible following the female's return to the

colony. Following the PM migration, females were resighted daily to establish an accurate pupping date, and instruments were not recovered until at least 5 d postpartum to allow the mother-pup bond to develop and to minimise the chance of separations.

As most females spent time on shore post deployment and/or pre-recovery, corrections were necessary to estimate mass at departure and arrival. This correction was based on equations derived from serial mass measurements of fasting female seals from previous studies (mass change [kg d^{-1}] = $0.51 + 0.0076 \times \text{mass}$, $n = 27$, $r^2 = 0.79$, $p < 0.01$; D. Crocker & D. Costa unpubl.). For PM recoveries, the mass of the pup at recovery was added to that of the female. Adipose and lean tissue gain was estimated from mass change and body composition, assuming body composition at arrival (or departure) was similar to that during the recovery (or deployment) and that the pup 5 d postpartum was 13% adipose tissue (Crocker et al. 2001).

Foraging success was measured as mass gain, energy gain or their respective rates across the entire migration. Energy gain was estimated assuming adipose tissue was 90% lipid and lean tissue was 27% protein (Crocker et al. 2001) and a gross energy content of 37.3 kJ g^{-1} for lipids and 23.5 kJ g^{-1} for protein. These estimates of body composition have been validated previously with dilution of isotopically labelled water (Webb et al. 1998).

Data handling. Satellite locations were obtained from Service Argos (Toulouse, France, and Landover, Maryland, USA) and were filtered using a basic speed filter of 10 km h^{-1} (McConnell et al. 1992). Alternate locations provided by Service Argos were used when appropriate. The resulting tracks were then interpolated every 5 min using a Bezier curve with $\mu = 0.1$ following Tremblay et al. (2006). Interpolation was necessary for a more accurate calculation of fractal dimension along the tracks. Furthermore, interpolation of tracks based on multiple locations can actually be more accurate than the underlying individual locations due to noise averaging, especially when temporal separation between locations is small (Lonergan et al. 2009).

Tracking statistics, including total track length (km), distal point from the colony (km), track duration (d) and mean transit rate (km h^{-1}) were calculated from the interpolated tracks, and compared for differences between migrations and years.

The fractal landscape method was used to identify ARS for each interpolated track following the methods of Tremblay et al. (2007). This approach uses fractal geometry to quantify how well an animal's search pattern covers a region or plane of interest both spatially and temporally. Given this, we felt it necessary that all ARS contain at least 3 Argos location fixes, and we removed any ARS that contained less than 3 original,

speed-filtered Argos locations. ARS were further modified, as Tremblay et al. (2007) noted that low numbers of raw ARGOS locations received per day may result in an overestimate of the area of ARS by a factor of up to 2.2 for elephant seals. To account for this, we corrected the radius of each ARS (and hence its area) using $y = -0.07908x + 2.605$, derived from the data presented by Tremblay et al. (2007), where y = correction factor, and x = mean number of raw ARGOS locations d^{-1} for each female. Several statistics representing searching behaviour were calculated for each ARS: number of ARS in each migration, time spent in ARS (d), distance travelled in ARS (km), and area of ARS (km^2). These ARS characteristics were then compared to measures of energy gain.

Because the boundaries of climate scale hydrographic features move seasonally, ecoregions were assigned dynamically following Weng et al. (2008), based on Longhurst (1998). To determine which of the 3 latitudinal ecoregions females were using on each migration, we extracted a value of sea surface temperature (SST) for each ARS using the mean position of the ARS and the midpoint of time spent in that ARS. SST data were obtained from <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp> and were blended over 5 d at a spatial scale of 0.1° from multiple sources, comprising Moderate Resolution Imaging Spectroradiometer (MODIS), Advanced Very High Resolution Radiometer (AVHRR) Imager, the Advanced Microwave Scanning Radiometer (AMSR-E) and NOAA's Geostationary Operational Environmental Satellite (GOES) Imagers. We assigned ARS to the Subarctic Gyre (SAG) if $\text{SST} \leq 12^\circ\text{C}$; the Transition Zone (TZ) if SST was 12.1 to 17.9°C ; and the Subtropical Gyre (STG) if $\text{SST} \geq 18^\circ\text{C}$ (Longhurst 1998). Neritic regions were defined by their proximity to the coast, with the Coastal Alaska Downwelling Region (CADR) being waters within 150 km of the coast and north of 48°N , and the California Current Upwelling Region (CCUR) south of 48°N and up to 1000 km from the coast at the southern margin, and 500 km from the coast at the northern margin (Longhurst 1998). Each female was designated to a single ecoregion based on the ecoregion in which she spent the greatest total time in ARS.

Analyses. Annual differences and differences between migrations in foraging success, tracking statistics and ARS characteristics were examined using linear mixed models with individual seal as a random effects 'subject' term. Model residuals were examined for approximate normality for all tests. Processing of tracking and environmental data was done using Matlab (Mathworks), and all models were run using SAS software, Version 9.1 of the SAS System for Windows.

RESULTS

From 75 deployments, 6 females failed to return to the colony and none of these animals has been sighted at Año Nuevo since. Of the remaining 69 deployments, 6 collected very little or no tracking data. Ultrasound (and hence energy gain measurements) were not collected for 2 females, and a further 9 failed to exhibit ARS behaviour and were removed from the analysis. This resulted in a dataset of ARS with accompanying measures of foraging success from 52 adult female northern elephant seals (PM 2004 = 14, PB 2005 = 11, PM 2005 = 16, PB 2006 = 11).

Foraging success

Mass and energy gain were significantly greater during the PM migration (282 ± 38 kg and 4444 ± 642 MJ, respectively) than the PB migration (77 ± 19 kg and 1254 ± 483 MJ; $F_{1,2} = 197.4$, $p < 0.005$ mass gain and $F_{1,2} = 185.1$, $p < 0.01$, energy gain). Due to the significant difference between migrations and because of the temporal distribution of sampling periods, annual comparisons were made only within migration (i.e. PB or PM). Thus, we limited comparisons to PM 2004: PM 2005 and PB 2005: PB 2006 when investigating annual effects.

Tracking, ARS and ecoregions

Satellite data from 52 females were used to calculate basic tracking statistics. Total track length and distal point from the rookery were significantly greater during the PM migration than the PB migration (Table 1, Fig. 2; $F_{1,2} = 90.0$, $p = 0.01$, and $F_{1,2} = 17.68$, $p < 0.05$).

Transit rates were significantly greater during the PB than the PM migration (Table 1, $F_{1,2} = 34.7$, $df = 1$, $p = 0.03$).

In total, 283 ARS were identified following Tremblay et al. (2007). Time spent in ARS ($F_{1,2} = 629.0$, $p < 0.001$) and the distance travelled within ARS ($F_{1,2} = 28.5$, $p = 0.03$) were significantly greater during the PM than the

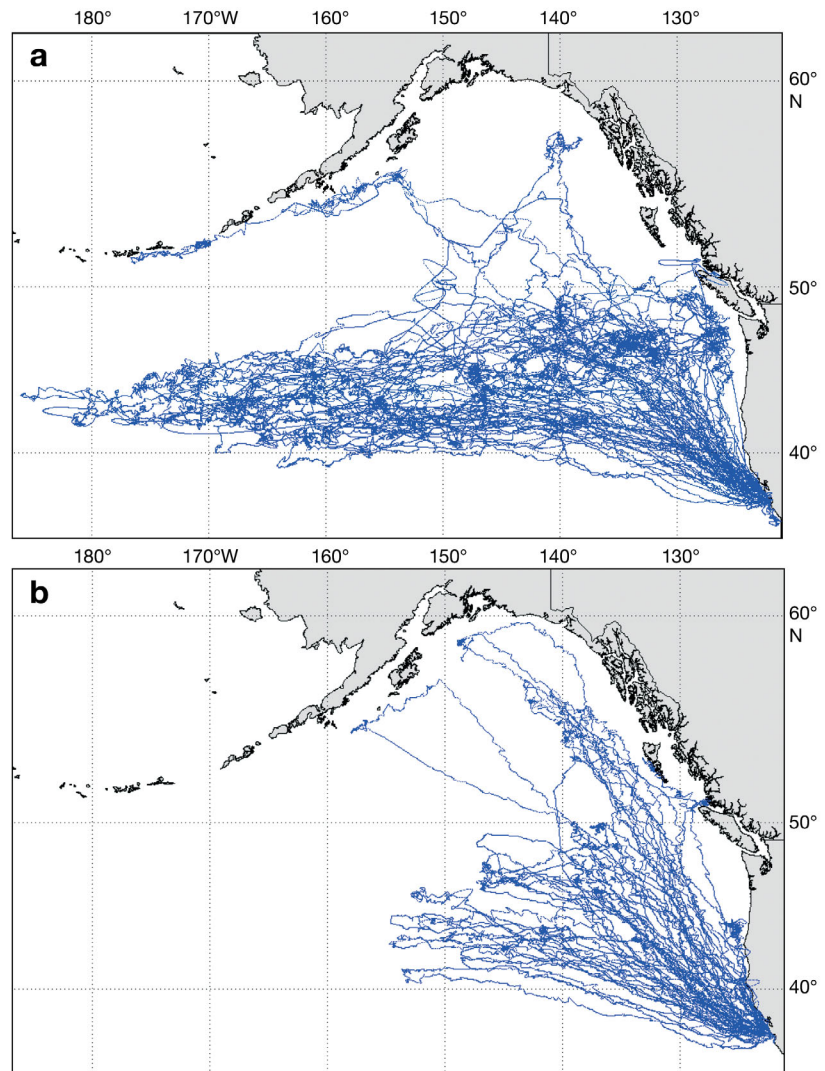


Fig. 2. *Mirounga angustirostris*. Satellite tracks for (a) all post-moult (PM) females (n = 33) between 2004 and 2005 and (b) all post-breeding (PB) females (n = 30) between 2005 and 2006

Table 1. *Mirounga angustirostris*. Summary statistics (mean \pm SD) for 52 females on their post-moult (PM) and post-breeding (PB) migrations for foraging success, tracking statistics and area-restricted search (ARS) statistics

Migration	Trip duration (d)	Mass gain (kg)	Energy gain (MJ)	Total track length (km)	Distal point (km)	Mean transit rate (km d ⁻¹)	No. of ARS	Time in ARS (d)	Distance travelled in ARS (km)	Area of ARS (km ²)
PM	224 \pm 13	282 \pm 38	4444 \pm 642	12578 \pm 2291	3236 \pm 1057	2.52 \pm 0.61	7 \pm 3	4.42 \pm 2.48	178 \pm 67	395 \pm 216
PB	79 \pm 8	77 \pm 19	1254 \pm 483	6954 \pm 1247	2266 \pm 525	3.75 \pm 0.54	3 \pm 2	2.44 \pm 1.44	166 \pm 75	653 \pm 471

PB migrations. There was no difference in the number of ARS ($F_{1,2} = 15.62$, $p = 0.06$) between migrations, but the spatial extent of ARS (area of circle) was larger on the PB than the PM migration (Table 1, Fig. 3, $F_{1,2} = 7.55$, $p = 0.01$). There were no significant annual differences found for any of the variables examined; hence, both years of PM and PB data were combined and considered together for all other analyses.

Locations of ARS revealed the TZ as an important basin-scale hydrographic feature for females on their PM trip, as 65% of ARS on this migration occurred in the TZ (Fig. 3a). During PB migrations, the SAG was the most extensively used hydrographic ecoregion

(74% of ARS on this migration, Fig. 3). Total time spent in ARS was significantly correlated with energy gain (Fig. 4), but migration was found to have a significant and dominant effect on this result (analysis of covariance [ANCOVA], $F_{1,2} = 90.34$, $p < 0.001$). When controlling for migration, the relationship between time spent in ARS and total energy gain was not significant for PB ($p = 0.89$) or PM ($p = 0.17$) data (Fig. 4). The strong effects of migration may be an artefact of the longer duration of the PM migration. To account for this, we considered the rate of energy gain in relation to hydrographic ecoregion. There were no differences among rates of energy gain (MJ d^{-1}) and the ecoregion in which ARS were located (Fig. 5). However, the lowest variability in rates of energy gain was evident when ARS were focused in the TZ, and the highest variability in rates of energy gain when ARS were focused in the SAG (Fig. 5).

DISCUSSION

Foraging success

There was wide variability in foraging success that was independent of location or ARS characteristics. Foraging success was greater during the PM migration than the PB migration, as has been found previously (Le Boeuf et al. 2000). Females in the current study also displayed rates of mass gain during the short PB migration similar to what Le Boeuf et al. (2000) found for mean rate of mass gain during long PM migrations between 1995 and 1997 (0.96 kg d^{-1}). This may reflect an upswing in female mass gain, perhaps in sync with postulated improved foraging success associated with the cold water regime of the Pacific Decadal Oscillation (Le Boeuf & Crocker 2005).

Tracking, ARS and ecoregions

We hypothesised that searching behaviour (characteristics of ARS) would vary by ecoregion used, possibly indicating different prey species distributions in each ecoregion. We found that females ranged farther on their PM migrations than their PB migrations (Figs. 2 & 3). Although these differences

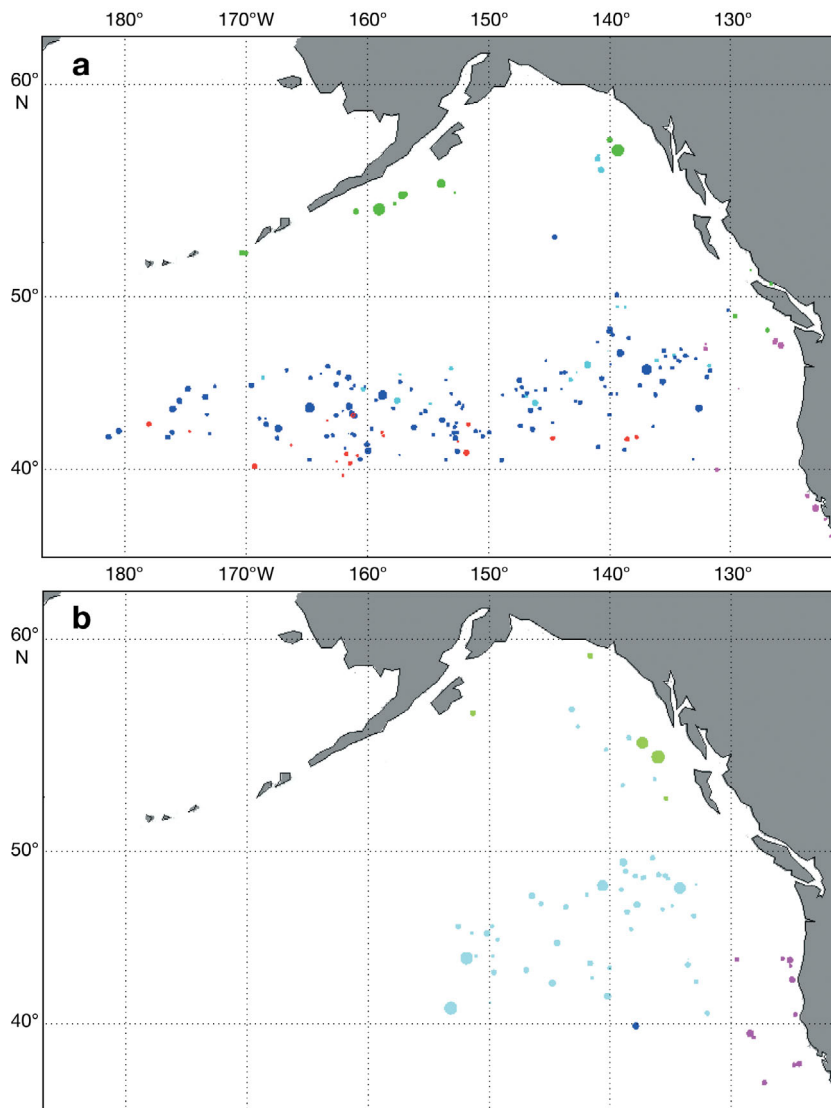


Fig. 3. *Mirounga angustirostris*. All area-restricted searches (ARS) from (a) 30 post-moult (PM) migrations and (b) 22 post-breeding (PB) migrations. Each circle represents 1 ARS, and the circle area is proportional to the area covered by the ARS. Colours indicate ecoregion. Red: Subtropical Gyre (STG), blue: Transition Zone (TZ), cyan: Subarctic Gyre (SAG), magenta: California Current Upwelling Region (CCUR), green: Coastal Alaska Downwelling Region (CADR)

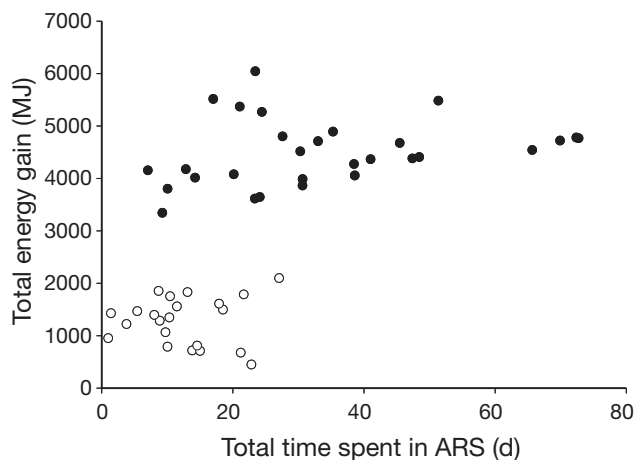


Fig. 4. *Mirounga angustirostris*. Significant relationship between total time at sea spent in area-restricted search (ARS) and total energy gain for all ARS on both migrations ($y = 1713.53 + 5643x$, $r^2 = 0.37$, $F = 29.10$, $df = 1$, $p < 0.0001$). However, analyses of covariance revealed that migration (post-moult [PM, ●]; post-breeding [PB, ○]) drives this relationship and, when considered by migration, total time in ARS was not significantly correlated to total energy gain (PB: $y = 1261.80 + 1.94x$, $r^2 = 0.0009$, $F = 0.02$, $df = 1$, $p = 0.89$. PM: $y = 4195.62 + 8.68x$, $r^2 = 0.07$, $F = 1.96$, $df = 1$, $p = 0.17$)

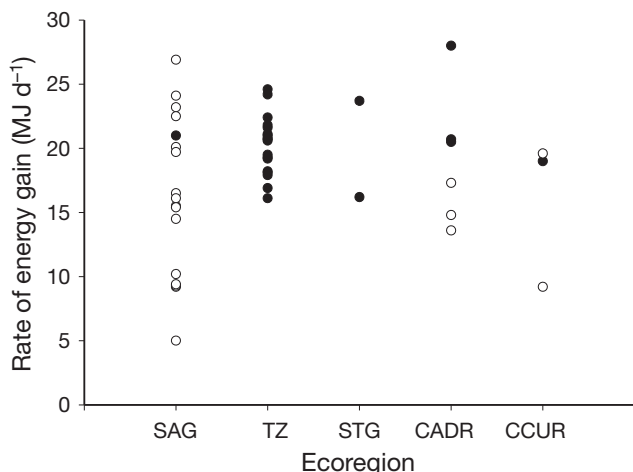


Fig. 5. *Mirounga angustirostris*. Variation in rates of energy gain for post-moult (PM, ●) and post-breeding (PB, ○) migrations, in relation to ecoregion. SAG: Subarctic Gyre, TZ: Transition Zone, STG: Subtropical Gyre, CADR: Coastal Alaska Downwelling Region, CCUR: California Current Upwelling Region. Each dot represents a single female that was assigned to a single ecoregion based on greatest total time spent in area-restricted search (ARS)

are likely an artefact of the shorter duration of the PB migration which did not give females enough time to exploit more distant areas, transit rates were higher on the PB than the PM migrations, implying that females could cover more ground than expected on the PB migration by just comparing days at sea. However, higher transit rates may be related to the lower foraging suc-

cess seen on the PB migration. If females fail to find adequate prey patches, an overall increase in transit rate would be expected. Both Le Boeuf et al. (2000) and Kuhn et al. (2009) have shown that slow transit rates correlate with increased foraging success in this species.

Females exhibited fewer ARS on the PB migration than the PM migration. Perhaps with less time to find subsequent patches, females increase their searching effort within a smaller number of patches on the PB migration. Interestingly, females travelled significantly farther within ARS on the longer PM trip than on the shorter PB trip, but ARS covered a significantly larger area on the PB than the PM migration (Table 1). The distribution of resources within a patch will affect the way a female searches for prey. The females did not spend more time in ARS on the PB migration (Table 1); thus, it is possible that resources are less aggregated at this time of year and females employ a different searching strategy to obtain sufficient resources. Some of these strategies are successful; rate of energy gain on the PB migration can be similar to that of the PM migration (Fig. 5). Thus, characteristics of searching behaviour did vary by ecoregion used, but the results were highly dependent on whether the female was on her PB or PM migration.

The distinct change in searching behaviour and positive trend between time in ARS and foraging success on PM migrations (Fig. 4) imply that ARSs represent important foraging regions for female elephant seals. However, determination of their exact ecological significance will require further investigation. Our results indicate that ARS were not pivotal to foraging success, as neither mass nor energy gain (Fig. 4) were significantly correlated with an increased time spent in ARS. Weimerskirch et al. (2007) also found a lack of correlation between ARS and feeding events when using a direct measure of feeding, stomach temperature telemetry, and high quality GPS tracking data in wandering albatrosses *Diomedea exulans*. Additionally, Bestley et al. (2008) found no relationship between direct measures of feeding and time spent within a given area in southern bluefin tuna *Thunnus maccoyii*. It is possible that ARS regions do not represent the only areas important for foraging success of apex predators in a patchy environment. In fact, Weimerskirch et al. (2007) found that over 75% of feeding events of albatross occurred outside ARS.

Differences between migrations were seen with respect to hydrographic ecoregions utilised by the females (Fig. 3), supporting our second hypothesis. However, the switch from most females using the TZ on their PM migration, to use of the SAG on the PB migration may simply be a result of the dynamic availability of these ecoregions relative to the location of the

colony, rather than an explicit choice of females for a particular ecoregion. This assertion is supported by the geographic overlap of the tracking data between migrations (Fig. 2). Additionally, with less time at sea on the PB migrations to acquire resources, females finding patches closer to the colony did not venture farther offshore to the TZ. Given the longer duration of PM migrations, females were able to venture farther in search of more productive patches. Four females exclusively used the TZ on their PM migrations, implying that perhaps some females identify this as a productive feature and may take a direct route to exploit this region. A higher use of more distant frontal zones has been shown in least auklets *Aethia pusilla*, presumably due to higher densities of preferred prey species at the front, rather than an absence of suitable prey species closer to shore (Russell et al. 1999). Within the TZ, one or several fronts may occur at any given time, and there can be large variability in the mesoscale hydrostatic stability in the upper ocean in this zone (Roden 1991). Frontal zones are known to concentrate nutrients and aggregate fish and squid (Lefevre 1986, Russell et al. 1999), an important elephant seal prey source (Condit & Le Boeuf 1984, Antonelis et al. 1987), as well as other vertebrate predators (Field et al. 2001, Polovina et al. 2001). The heterogeneity of the TZ makes it an efficient resource to exploit because an individual will not have far to travel before encountering a new patch. Mesoscale eddies in this region act to locally enhance productivity at intermediate temporal and spatial scales, and submesoscale vortices on the flanks of transient jets may create productive patches on the order of a few km (Roden 1991). This environmental heterogeneity creates habitat diversity for potential prey of elephant seals, including fish and squid, given their thermal tolerances and preferences (Brandt 1981, 1983, 1993). Indeed, diversity of fish larvae has been shown to be highest in the TZ and lowest in the SAG (Norcross et al. 2003).

In contrast, although the SAG contains several mesoscale, anti-cyclonic eddies such as the Haida and Sitka eddies (Tabata 1982, Musgrave et al. 1992, Crawford 2002) that enhance production (Whitney & Robert 2002, Crawford et al. 2005) and may be important features for foraging elephant seals (Simmons et al. 2007), they are also more patchily distributed relative to the lower amplitude mesoscale eddy field of the TZ (Roden 1991). Thus, there may be a strategic trade-off between a low encounter rate of potentially higher quality patches in the SAG and a high encounter rate of potentially lower quality patches in the TZ. This trade-off may be particularly relevant to a capital breeder such as the northern elephant seal and may at least partially explain the differences seen in the variability of success in adult females between these 2 regions (Fig. 5).

Our third hypothesis, that foraging success would vary with higher rates of energy gain associated with more productive, higher latitude ecoregions, was not supported by our results; overall, females using the SAG did not show higher rates of mass gain than females using the TZ (Fig. 5). However, there was greater variability in rates of energy gain during the PB migration, when the females were using the SAG almost exclusively, than during the PM migration, when the TZ was primarily used (Fig. 5). This could be explained by and could highlight the advantages of a capital breeding strategy. On the PB migration, the females have to contend with a combination of less time at sea foraging and a greater threat of 'boom or bust' given the more patchy distribution of resources in the SAG described above. Meanwhile, as females have up to 8 mo to amortise energy requirements on the PM migration, the end result may be lower variability in rates of energy gain. Alternatively, the lower variability may be due to the use of the TZ, with a higher encounter rate of lower quality patches, by most females at this time of year. Either explanation highlights the value of a capital breeding strategy in an organism exploiting an environment with a patchy distribution of resources.

It has been previously noted that only a few females forage in the coastal zone, but interestingly, their foraging success is often comparable to that of the much larger adult males (Le Boeuf et al. 2000, Simmons et al. 2007). In this study, only 9 females exhibited ARS primarily in coastal zones, and these zones were exploited on both migrations (Fig. 5). Although one of these females did show the greatest rate of energy gain of any animal in the study, in general, success of females using coastal zones did not significantly differ from that of females using other ecoregions on either migration. Coastally foraging females remain rare in this population, and while several reasons for this have been proposed, including competition with males and/or increased risk of predation on the continental shelf (Le Boeuf & Crocker 1996, Le Boeuf et al. 2000), there has been no explicit investigation of these ideas.

Other predators in the North Pacific

Comparison of tracking data from northern elephant seals to other apex predators using the North Pacific might suggest significant overlap in habitat selection and potentially high levels of interspecific competition. For example, tracks from salmon sharks *Lamna ditropis* (Weng et al. 2008), Laysan *Phoebastria immutabilis* and black-footed albatross *P. nigripes* (Hyrenbach et al. 2002) and loggerhead turtles *Caretta caretta* (Polovina et al. 2000, 2001) all reveal that these predators

spend time in overlapping pelagic and coastal areas of the North Pacific.

Weng et al. (2008) found that, in contrast to the elephant seals in our study, time spent by salmon sharks in both the CADR and the CCUR was likely important for foraging, while the sharks mainly transited through the SAG and TZ pelagic ecoregions. The ecological significance of these large-scale ecoregions for Laysan and black-footed albatrosses varies between species and with their annual reproductive cycles. During the brooding period, the STG is primarily used by black-footed albatrosses, while Laysan albatrosses focus their foraging efforts in the colder TZ region (Hyrenbach et al. 2002). During the chick-rearing period, black-footed albatrosses exploit the CCUR, whereas Laysan albatrosses venture further north to the SAG and northern TZ (Hyrenbach et al. 2002). The physical-biological coupling that may be driving these patterns was found to be scale-dependent and highlighted the need to examine behaviours at both macro-mega scales (100 to >10 000 km) and coarse meso-scales (~100 km) to understand underlying water mass distribution, as well as recognising smaller features that may be locally enhancing productivity and aggregating prey (Hyrenbach et al. 2002). Loggerhead turtles apparently follow specific frontal features of the TZ, such as the TZCF (operationally defined at 0.2 mg m^{-3} ; Polovina et al. 2001), or specific thermal fronts within the TZ (Polovina et al. 2000), deriving all necessary resources from aggregations of prey at these frontal structures.

Although a simple comparison of tracking data may indicate species overlap and potential competition, a closer examination of the ecological significance of the different zones to each organism reveals the importance of scale and the complexity of the marine ecosystem and highlights the challenges of predicting responses of such predators to local, seasonal, annual and inter-decadal climate changes.

CONCLUSIONS

Hydrographic ecoregions of the North Pacific used by female elephant seals on each of their foraging migrations were identified and linked with foraging success measured by mass and energy gain. There was wide variability in foraging success that was independent of geographic location but was likely driven by the hydrographic ecoregion used and was highly influenced by migration. Lower variability in rates of energy gain on the PM migration highlights the benefit of a capital breeding strategy when foraging in a heterogeneous and dynamic system. Operating over broader temporal and spatial scales in this environ-

ment, females were able to recover body condition and obtain resources to sustain them through the next fasting period using a variety of ecoregions and searching strategies. Identification of ARS areas was invaluable as a starting point to consider the successful use of the North Pacific by adult females in relation to the major hydrographic ecoregions, and a vital first step to further our understanding of habitat selection and potential responses to climate change in this wide-ranging apex predator.

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