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Persistence of forage fish 'hot spots' and its association with foraging Steller sea lions (*Eumetopias jubatus*) in southeast Alaska

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Abstract

Whereas primary and secondary productivity at oceanic 'hotspots' may be a function of upwelling and temperature fronts, the aggregation of higher-order vertebrates is a function of their ability to search for and locate these areas. Thus, understanding how predators aggregate at these productive foraging areas is germane to the study of oceanic hot spots. We examined the spatial distribution of forage fish in southeast Alaska for three years to better understand Steller sea lion (*Eumetopias jubatus*) aggregations and foraging behavior. Energy densities (millions KJ/km^2) of forage fish were orders of magnitude greater during the winter months (November–February), due to the presence of schools of overwintering Pacific herring (*Clupea pallasi*). Within the winter months, herring consistently aggregated at a few areas, and these areas persisted throughout the season and among years. Thus, our study area was characterized by seasonally variable, highly abundant but highly patchily distributed forage fish hot spots. More importantly, the persistence of these forage fish hot spots was an important characteristic in determining whether foraging sea lions utilized them. Over 40% of the variation in the distribution of sea lions on our surveys was explained by the persistence of forage fish hot spots. Using a simple spatial model, we demonstrate that when the density of these hot spots is low, effort necessary to locate these spots is minimized when those spots persist through time. In contrast, under similar prey densities but lower persistence, effort increases dramatically. Thus an important characteristic of pelagic hot spots is their persistence, allowing predators to predict their locations and concentrate search efforts accordingly.
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Keywords: Steller sea lions; Herring; Hot spot persistence; Foraging effort

1. Introduction

The ability to predict the location of prey is an important component of foraging behavior of predators (Webb and Marcotte, 1984; Grand and Grant, 1994; Siems and Sikes, 1998), and this is nowhere more relevant than for air-breathing

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vertebrates that forage at sea. Faced with physiological and energetic constraints in acquiring prey that may be ephemerally available in time and patchily distributed in a three-dimensional water space, predictable distributions of prey allow foraging marine mammals and birds to concentrate search efforts in specific areas during specific time periods, facilitating efficient foraging (Irons, 1998; Davoren et al., 2003).

When an area is located that is sufficiently profitable, predators will remember their locations (Kacelnik and Krebs, 1985; Milinski, 1994; Irons, 1998), and concentrate short- or long-term search efforts accordingly (i.e. long-term area-concentrated search; Bell, 1991; Bonadonna et al., 2001). This behavior is highly adaptive because foraging efficiency is often strongly linked to fitness, particularly when foraging distance is spatially constrained. For example, many pinnipeds and birds must return to rookeries or breeding colonies on a regular basis to feed offspring. The inability to efficiently find productive foraging areas may result in elevated rates of starvation to offspring (Costa et al., 1989) or abandonment by incubating adults (Weimerskirch, 1995; Arnold et al., 2004).

One mechanism that can contribute to the predictability of prey is when profitable foraging patches persist through time. Here predators learn these locations (Kamil, 1983) and base their search efforts on spatial memory and the expectation of productive foraging (Noda et al., 1994). Persistence may occur at small time scales, allowing predators to predict the location of prey during consecutive foraging bouts (Bonadonna et al., 2001), or at larger time scales, such that seasonal migrations are directed around profitable foraging areas. In the absence of persistence of important foraging areas, predators must approach each forging trip without knowledge of the location of the important foraging habitat. Persistence thus may be fundamental for predators to locate productive prey areas efficiently.

Although many studies have concluded that the ability to predict the distributions of prey is relevant to the fitness and foraging ecology of marine mammals (Le Boeuf et al., 2000; Guinet et al., 2001; Sinclair and Zepplin, 2002) and sea birds (Skov et al., 2000), very few studies have quantified prey persistence for marine predators, particularly across larger time scales (months, seasons, years). Studies will often quantify movements of pelagically foraging predators, and infer from these data qualitative estimates about the abundance and distribution of prey (Weimerskirch et al., 1997; Guinet et al., 2001).

In this study we quantified the monthly distribution of forage fish in pelagic environments of southeast Alaska across three years using hydroacoustic surveys methods, while simultaneously collecting data on the distribution of a common marine predator, the Steller sea lion (*Eumetopias jubatus*). Our goal was to understand better how the spatial and temporal dynamics of prey influence the foraging ecology and behavior of predators that utilise them. Specifically, we quantified (1) the distributions of pelagic forage fish, i.e. the existence of prey 'hot spots'; (2) whether these hot spots persisted within and across seasons, and (3) the location of foraging sea lions relative to hot spot persistence. We also constructed a simple spatial model to examine how foraging effort may be influenced by the density or persistence of prey hot spots.

Although our study was conducted at much smaller spatial scales than typical of 'hot spot' analysis of open ocean pelagic environments (Etnoyer et al., 2004), we hoped to gain insight into characteristics of prey distributions that may influence their utilization by foraging marine predators.

2. Methods

2.1. Study area

Acoustic surveys were conducted in Favorite Channel, upper Lynn Canal, southeast Alaska, between Tee Harbor (58°43′ W; 134°77′ N) and Vanderbilt Reef (58°58′ W, 134°97′ N) on a monthly basis between June 2001 and May 2004 (Fig. 1). This area was chosen because it is relatively sheltered, facilitating year-round surveys using small, cost-effective vessels, and because it encompasses a variety of habitats (depth range between 5 and 305 m; average depth = 60 m), typical of areas used by foraging sea lions in southeastern Alaska. It also includes a site (Benjamin Island) used as a seasonal haul-out, where up to 600 sea lions are present from October until April (Womble and Sigler, in press).

2.2. Estimates of monthly prey distributions

To quantify pelagic fish distributions we used a portable 38 kHz Simrad echo-integration system with
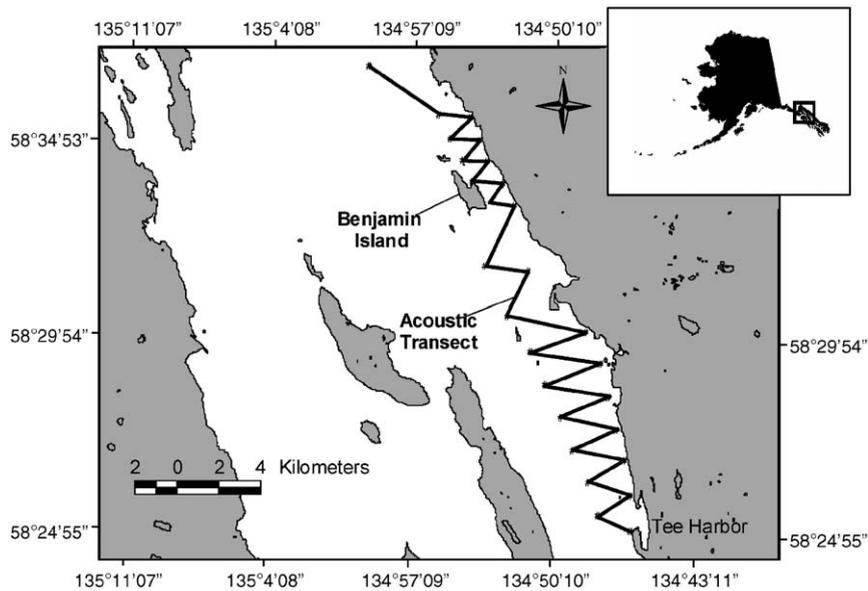
Fig. 1. Location of hydroacoustic and Steller sea lions surveys, upper Lynn Canal, southeastern Alaska.

a 12° beam angle, towed at 11 km/h. The echo-integration system was periodically calibrated with a sphere of known acoustic density. We simultaneously collected location data using a Garmin Global Positioning System with location accuracy within 10 m. All surveys began in the morning after daybreak and concluded before dark. Some fish species, particularly herring, undergo diurnal migrations through the water column (Huse and Ostrowski, 1998; Huse and Korneliussen, 2000), thereby changing the distribution and density estimates. However, we chose to sample during the daylight hours (between 0800 and 1700) because it facilitated observations of forging sea lions while collecting acoustic data. Daytime acoustic surveys also will minimize the potential for vessel avoidance by species near the surface, which for herring, may be substantial (Olsen et al., 1983; Huse and Korneliussen, 2000). Further, as our goals were to determine relative indices of abundance over time, rather than absolute estimates, surveys conducted only during the day had similar error across all sampling periods thereby minimizing the impacts on our results (Huse and Korneliussen, 2000). Finally, although sea lions will forage at night, they also commonly forage during the day, and thus we felt that initial efforts for relating characteristics of prey distributions relative to sea lion distributions would be most fruitful during daylight hours.

Length, weight, and species classification data, necessary complements to acoustic data, were collected quarterly with midwater trawls deployed from the 18-m F/V *Solstice* from September 2001 to March 2002 and the 31-m F/V *Viking Storm* from May 2002 to May 2004. Two mid-water trawls were used, a 164 Nordic rope trawl with 1.5-m² alloy doors, 7 m height and 17 m width with a 19 mm mesh codend liner and a mesh wing 25/21/64 trawl with 3.0-m² alloy doors, 11 m height and 29 m width with a 32-mm mesh codend liner.

The acoustic data were classified by species (using the mid-water trawl data to verify species found during acoustic surveys), integrated for 0.183-km length intervals and 10-m depth intervals, and corrected for instrument calibration using the echo-integration software SonarData Echoview. To convert the acoustic scattering (NASC) to fish density in numbers, estimates of acoustic reflectivity for single fish were estimated using length- and species-specific target strength (TS) equations of the generalized form of $TS = 20 \log_{10} L + b$ (MacLennan and Simmonds, 1992), where $b = -66$ for walleye pollock (*Theragra chalcogramma*) (Traynor, 1996) and $b = -65.4$ for Pacific herring (*Clupea pallasi*) (Ona, 2003). NASC and TS values for herring were further adjusted for acoustic shadowing and depth compression of the air bladder (Ona, 2003). TS values were transformed to backscattering cross-section, $\sigma_{bs} = 4\pi 10^{TS/10}$ such that fish density was computed by dividing NASC by σ_{bs}. Fish density in weight equals density in number

multiplied by average weight and is expressed in units of $kg\,km^{-2}$.

Fish density in weight was then converted to nutritional energy using season-, size-, and species-specific energy conversions determined in a companion study (Vollenweider and Heintz, in press). We present results of prey in terms of energy such that they represented a common 'currency' upon which marine mammals and birds are known to base forage decisions (Kacelnik and Krebs, 1985). Whereas variability in mass-specific energy content of walleye pollock and herring was approximately 2-fold (7.7 kJ/g vs. 4.3 kJ/g, respectively; see Vollenweider and Heintz, in press), biomass density in an area could vary by several orders of magnitude. The variation in prey energy density was due mostly to variation in biomass present of a given species, rather than seasonal and species-specific differences in mass-specific energy content. Consequently, monthly biomass and energy estimates were highly correlated (pollock: $r^2 = 0.97$; herring $r^2 = 0.99$; Gende and Sigler, in press), and thus we report results only in terms of nutritional energy. Nutritional energy is expressed in units of millions of kJ/km^2 by species, 0.183-km transect, and 10-m depth interval.

2.3. Data analysis

We first grouped acoustic data into small transects of 0.19 km (0.1 nm) of 10-m depth intervals, and then integrated across the water column, such that each transect had an estimate of prey energy density (in millions of kJ/km^2; see Fauchald et al., 2000; Davoren et al., 2003). The transect data were then grouped into blocks, where each block encompassed a latitudinal minute (e.g. $58°25'$ to $58°26'$, a distance of 1.83 km). We then computed means (and standard errors) using the energy density estimates from transects as data points that constitute each 1-min block (each block contained at least six transects). As a result of this blocking procedure, the study area had a maximum of 16 latitudinal blocks (for each month surveyed), each with an average energy density. This is the spatial scale at which we conducted our analyses.

A block was defined as 'hot' if it supported greater than average prey densities, where the average was calculated for all blocks within that month (see similar procedures in Davoren et al., 2003). This resulted in a month-specific binary designation of each block as hot or not. We then summed across all months the number of times each

block was hot (see also Etnoyer et al., 2004). As all blocks were surveyed for 34 months (three years of surveys minus two months of equipment failures), each block could be 'hot' for up to 34 months maximum. Persistence of hot spots (blocks) was calculated by summing the number of months that block was hot divided by the total number of months it was surveyed. Note that we use the term 'blocks' synonymously with 'spot', so that our analysis is examining hot spot (or block) persistence.

We then examined the persistence of prey hot spots relative to the distribution of foraging Steller sea lions. During all acoustic surveys we recorded the location and activity (foraging, milling, traveling) of any observed sea lion. We classified sea lions as 'foraging' if they were observed consistently diving in an area, 'traveling' if sea lions were seen swimming at or near the surface in a consistent direction, and 'milling' if seen on the surface but not diving.

From these data we labeled whether each block contained a foraging sea lion or not. We used linear regression to explore the relationship between the presence of foraging sea lions and the persistence of prey hot spots. Although this analysis considered only 'foraging' sea lions, most of the sea lions seen were classified as foraging and thus results only changed slightly if we included sea lions from all behavioral categories.

2.4. Foraging effort model

Although we were able to document the location of foraging sea lions during our acoustic surveys, and thus determine whether they were associated with forage fish hot spots, we had no estimates of the amount of effort needed by sea lions to locate these hot spots. We thus constructed a simple, two-dimensional spatial model to examine how the density and predictability (persistence) of hot spots might affect foraging effort of a generalized predator. Hot spots were placed randomly within a 100×100 X–Y grid (10,000 cells) with the density varying between 1%, 5%, and 10% of all cells. Each cell with prey represented a non-depleting hot spot where, once found, the predator will have equal attack probabilities and capture success (Sih and Christensen, 2001), and can feed to satiation. Thus, density defines the number of equally productive hot spots within an area, rather than the number of prey within a spot (i.e. the foraging value of hot spots were equally high).

During the first time period, the distribution of hot spots was spaced randomly. During the

following time period, the hot spots were relocated a random distance and direction from their previous location. Predictability was controlled by setting the maximum distance the relocated prey could lie from its previous location. Distance was modeled as a random variable from a uniform distribution over the interval 0 to m, where m is the maximum distance. Small m-values imply high predictability and large m-values imply low predictability. For example, $m = 0$ implies that the prey are located in the same position (i.e. they persist) during consecutive time periods, whereas $m = 7$ implies that the prey are relocated up to seven cells away from its previous location. In other words, when productive prey locations move little from one time period to the next, they essentially persist through time. Thus there is an inverse relationship between prey persistence and the distance the prey move between time intervals. The tested range of m was 0–9 cells.

Predator foraging was modeled such that all searches began from a central place (e.g., rookery or colony). Step distance (the number of cells it moved in a straight line while searching) was modeled as a random variable from a uniform distribution over the interval 0 to n, where n is the maximum step length. Small n-values imply the predator searches a short linear distance before changing direction and large n-values imply the predator travels in a straight line for longer distances. The direction of each change was chosen at random. Although the tested range of n was 1, 5, and 10 cells, our results revealed that the relationship between relative effort and predictability was similar across all step lengths and thus we focus only on a step length of five.

During the first time period, we assumed the predator had no previous knowledge of the distribution of prey and thus a random search method was employed. Thereafter, we examined effort using two search modes: random forager vs. a Bayesian forager (sensu Kamil, 1983; Alonso et al., 1995). The Bayesian search mode used prior knowledge of the location of hot spots to guide its search efforts and expectation of successful foraging (Noda et al., 1994). The Bayesian search begins by the predator returning to the location (cell) where a prey was located during the previous time period. If a hot spot is not located, then a random search begins. Searching continues until a hot spot is located. The distance traveled is accumulated as the predator searches; the total distance traveled to locate a hot spot is a measure of foraging effort and inversely related to foraging efficiency, which is a central

component influencing the evolution of foraging behavior (Kacelnick and Houston, 1984).

Effort needed to locate a hot spot was examined relative to hot spot density (3 levels of 1, 5, and 10 productive hot spots per 100 cells) and prey predictability (10 levels, $m = 0, 1, \ldots, 9$). Crossing the factors results in 30 (3×10) scenarios. Each scenario was repeated 1000 times with the average distance traveled (foraging effort) computed for each scenario from the 1000 replicates. For comparative purposes, we graphed foraging effort of both Bayesian and random search methods as a function of density and predictability.

We present the results as unitless measures of predictability and foraging effort (could be time or energy). This abstraction allowed us to address the question of 'how does the density and persistence of productive foraging spots influence foraging effort?'

3. Results

A total of 34 acoustic surveys, conducted between June 2001 and May 2004, revealed that there were large seasonal differences in the pelagic prey energy in the study area (Fig. 2). During the winter months, November–February, the average energy density of pelagic prey was almost an order of magnitude greater than the average energy density in other months ($\bar{x}$ winter = 2101 million kJ/km^2, $\bar{x}$ non-winter = 211, $t = 4.86$, df = 32, $p < 0.001$). This was due predominantly to the presence of large schools of overwintering herring that moved into the area during the winter. Although many species were recorded during pelagic trawls, herring represented almost 97% of the total prey energy (and biomass) available in the study area during the winter, with walleye pollock making up most of the remaining prey.

3.1. Hot spot persistence

Given the large seasonal variation in prey energy distribution, we examined the location of pelagic prey 'hot spots' during the winter and non-winter months. During the winter, several areas were consistently characterized by large schools of herring. These areas, predominantly between $58° 27'$ W and $58° 29'$, supported above average prey densities during nearly 70% of the surveys, i.e., these hot spots persisted in 8 of the 12 winter surveys across three years (Fig. 3). In contrast, large schools of herring were consistently absent from several areas in the southern part of our study area (Fig. 3). Several
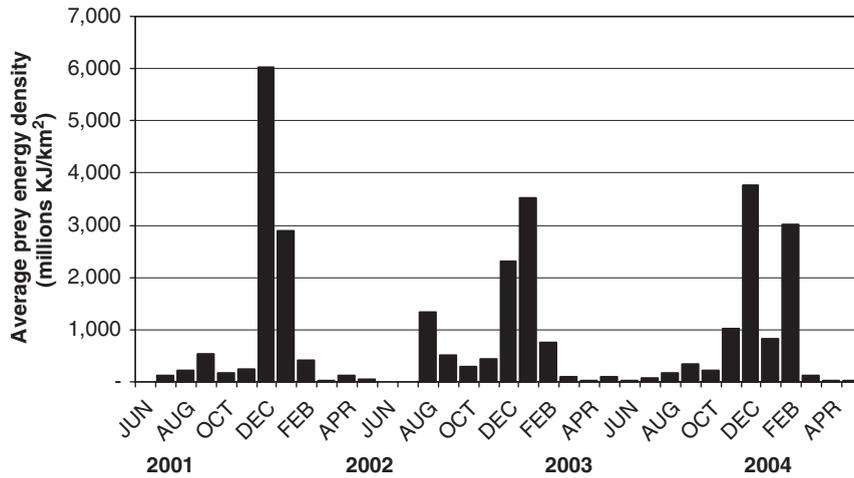
Fig. 2. Monthly prey energy in the study area, June 2001–May 2004.
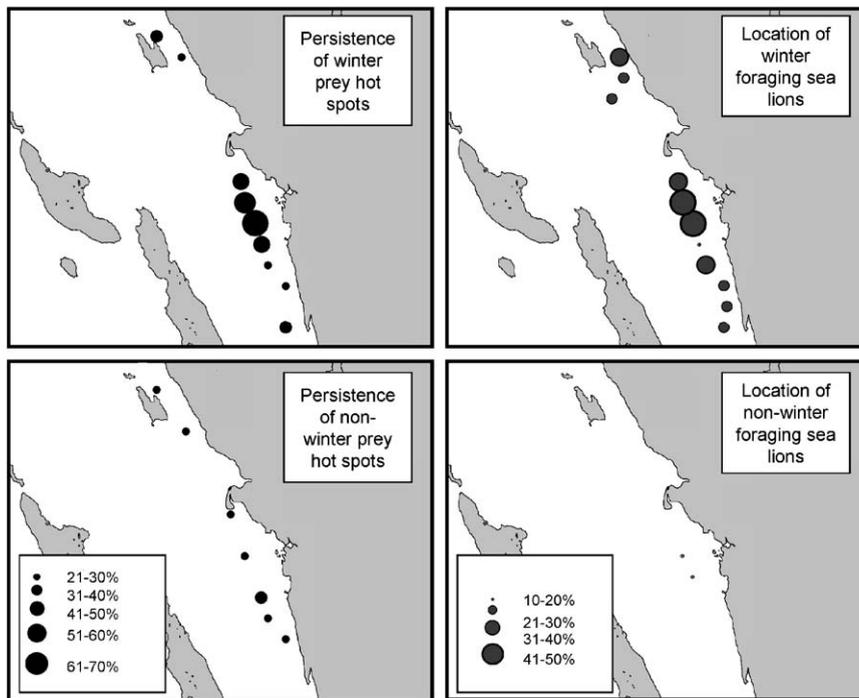
Fig. 3. The spatial distribution of foraging sea lions and hot-spot persistence during winter and non-winter months, upper Lynn Canal. Persistence was defined as the proportion of surveys when that spot supported above-average prey densities ('hot'). Sea lion distribution was defined by the proportion of surveys when a sea lion was observed foraging in that spot.

spots either never supported above average prey densities or were hot for only one of the 12 winter surveys, resulting in very low persistence.

In sharp contrast, blocks were hot for only an average of 18% of the observations during non-winter months. Persistence exceeded 30% for only one spot across the study area, i.e. this spot was hot for a total of seven of the 22 non-winter months it was surveyed).

3.2. Relationship between sea lion distribution and hot spot persistence

During acoustic surveys, a total of 278 sea lions were recorded during 61 observations. Aggregations of sea lions varied in size from several to more than 40. Although many sea lions were observed during the winter months, aggregations of up to 16 animals

were also seen during the non-winter months. Sea lions were mostly seen foraging (actively diving in one area) although some were observed milling in an area (not diving) or swimming rapidly at the surface (traveling).

During the winter months, there was a strong relationship between the persistence of hot spots and the probability of observing a foraging sea lion, although this relationship was absent during the non-winter months (Fig. 3). At these hot spots, we often observed sea lions diving consistently on the herring schools and, at times, were able to record their locations on the acoustic surveys. During the winter, over 40% of the variation in sea lion foraging locations could be explained by the variation in hot spot persistence (proportions arc-sine transformed; $F = 9.51$, df = 15, $p = 0.008$; Fig. 4). Similar results were found if we considered only foraging sea lions or all observations of sea lions (milling, traveling). In contrast, no relationship was observed with hot spot persistence and the location of foraging sea lion during the non-winter months, in part because hot spots were not nearly as persistent during this time (Fig. 3). The relationship between sea lion foraging observations during the non-winter months and hot spot persistence was not significant (proportions arc-sine transformed; $F = 0.1$, df = 15, $p = 0.75$; Fig. 4) (Fig. 5).

3.3. Foraging effort model

Our simple foraging model revealed that effort was generally a function of both the density and persistence of hot spots. When the density of hot spots was low, the effort necessary to locate prey was substantially increased as prey became more randomly distributed during consecutive time periods (Fig. 4A). In other words, foraging effort remained low (for Bayesian foragers) despite low density of hot spots because the spots persisted through time. Foraging effort was generally asymptotic, increasing until predictability was half of initial estimates at which point it was approximately similar regardless of changes in predictability. Random foragers did not benefit from persistence because they approached each foraging bout without knowledge of the location of productive foraging spots.

The asymptotic relationship between effort and persistence (for Bayesian foragers) was similar across all prey densities, although the relative benefit was much smaller at high densities. In fact, at the highest prey densities (Fig. 4C), having
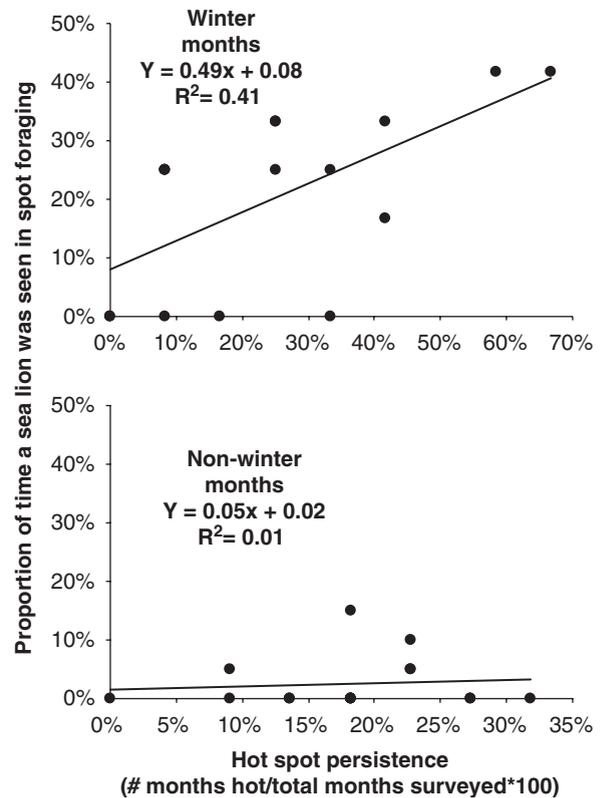
Fig. 4. Relationship between hot-spot persistence and the frequency with which Steller sea lions were seen foraging in those spots during the winter (November–February) and non-winter months (all other months; bottom). Each data point represented a 1.1 km block. The block was considered 'hot' if it had above average prey energy densities.

previous knowledge of the location of prey hot spots (Bayesian search) conferred only small decreases in foraging effort because foragers were more likely to randomly encounter hot spots.

4. Discussion

Much emphasis has recently been placed on identifying oceanic 'hot spots', i.e. areas of high pelagic productivity, because these areas also tend to be associated with aggregations of upper trophic level predators and thus have high conservation and management value (Etnoyer et al., 2004). Yet not all highly productive pelagic habitats support aggregations of top predators. In some cases this may simply be a function of the spatial extent of the area: a randomly searching predator increases the probability they will encounter this area if it is sufficiently large. Our results, however, suggest that
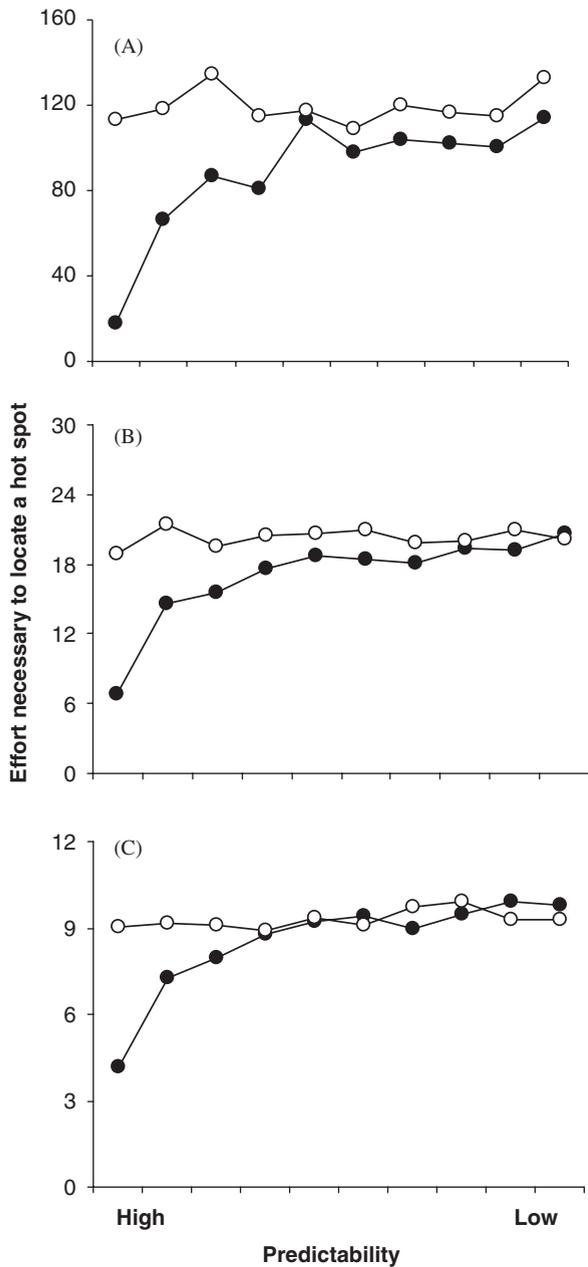
Fig. 5. Model results demonstrating the relationship between foraging effort relative to hot spot predictability under three scenarios of prey densities (A) 1% of all areas hot; (B) 5% of all areas are hot; and (C) 10% of all areas are hot. (●) indicates a Bayesian forager whereas (○) represents a randomly searching forager.

persistence of these hot spots may be an important attribute that allows pelagically foraging predators to locate and utilize these areas.

By conducting acoustic surveys on a monthly basis, we found that forage fish, primarily Pacific

herring, were highly aggregated, and these aggregations persisted in space and time. We labeled these areas 'hot spots' because they represented highly valuable foraging opportunities for top predators. However, this definition of a 'hot spot' differs somewhat from other studies because it was primarily a function of fish behavior, as opposed to trophic cascades at oceanic fronts or temperature gradients (Cairns and Schneider, 1990; Etnoyer et al., 2004). Herring are not feeding during the winter months because their primary prey, copepods, is at a very low abundance. Thus, herring tend to follow an energy conservation strategy, minimizing movements during this period (Corten, 2002; Ona, 2003). By March herring will begin to migrate en masse to spawning areas (Carlson, 1980), after which they subdivide into smaller foraging schools and disperse (Haegele and Schweigert, 1985), generally moving much more extensively in pursuit of ephemeral patches of copepods. This explains why there were comparatively fewer hot spots in the study area in the summer and why summer hot spots did not persist. It is thus not surprising that we rarely encountered aggregations of foraging sea lions during the summer.

In contrast, the winter months were characterized by large aggregations of Steller sea lions at these hot spots. That sea lions were found to consistently utilize certain areas is quite common for pelagically foraging vertebrates. Many studies have documented that marine mammals (Bondadonna et al., 2001; Guinet et al., 2001) and sea birds (Sagar and Weimerskirch, 1996; Irons, 1998) regularly commute to preferred foraging areas, and will use previous knowledge to help relocate these areas (Kenney et al., 2001). The aggregations of marine mammals at spawning areas of eulachon provide an excellent example of how predictable prey masses will attract predators on a seasonal basis (Marston et al., 2002). However, our results are insightful because it appeared that sea lions are responding to the persistence of prey hot spots rather than aggregating at the spots with the highest density.

For example, in November of each year the largest schools of herring were found in the northern part of our study area, near Benjamin Island. As the winter progressed, the largest schools had moved to the southern part of the study area, with little herring observed near Benjamin Island by late February (Gende and Sigler, in press). Thus, the location of the highest densities of prey (the hottest of the hot spots) varied across the study area

throughout the winter, i.e. the location of the highest density spots did not persist within a season. Yet sea lions were most often observed foraging in spots between $58°27'W$ and $58°29'$. These spots were not always characterized by the highest prey densities, but consistently had above average prey densities. This is the reason we found a relationship between prey spot *persistence*, rather than prey *density*. In fact, we found that the largest number of sea lions was associated with the highest densities of prey in only 6 of 12 winter surveys.

Our foraging model provided insight into why sea lions may be choosing the hot spots with the highest persistence. Foraging effort was markedly reduced when prey persistence was high because sea lions could return to the areas where they previously encountered high foraging success. Even small movements of these hot spots resulted in reduced foraging effort (and thus increased foraging efficiency) because it took sea lions little effort to 'find' these locations. Yet these benefits were not incurred when the density of hot spots was high, in part because even if a sea lion is employing a Bayesian foraging strategy by returning directly to the area of previous hot spots, they were likely to encounter a hot spot on the way by chance. This is why the foraging effort using a random search strategy was quickly just as efficient as a Bayesian search strategy at high prey densities.

5. Conclusions

Many studies have examined the foraging movement and habitat use by marine foraging birds and mammals, while others have examined the density and distribution of forage fish and lower trophic level aggregations. The analysis of hot spots combines these two disciplines. However, it is necessary to consider the mechanisms behind predator aggregations at these hot spots in order to predict how aggregations will vary across time and factors that may influence their use. Our results suggest that persistence may be an important attribute of hot spots because it allows top predators to predict the location of productive foraging habitats. We encourage other studies at larger spatial scales, particularly for open ocean pelagic environments, to test the applicability of these results.

Acknowledgements

References

Alonso, J.C., Alonso, J.A., Bautista, L.M., Munoz-Pulido, R., 1995. Patch use in cranes: a field test of optimal foraging predictions. Animal Behaviour 49, 1367–1379.

Arnold, J.M., Hatch, J.J., Nisbet, I.C.T., 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? Journal of Avian Biology 35, 33–45.

Bell, W.J., 1991. Searching Behaviour. Chapman & Hall, London.

Bonadonna, F., Lea, M.A., Dehorter, O., Guinet, C., 2001. Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazelle*. Marine Ecology Progress Series 223, 287–297.

Cairns, D.K., Schneider, D.C., 1990. Hot spots in cold water: feeding habitat selection by thick-billed murres. Studies in Avian Biology 14, 52–60.

Carlson, R., 1980. Aggregations of overwintering herring in Lynn Canal, southeastern Alaska. Transactions of the American Fisheries Society 22, 46–48.

Corten, A., 2002. The role of "conservatism" in herring migrations. Reviews in Fish Biology and Fisheries 11, 339–361.

Costa, D.P., Croxall, J.P., Duck, C.D., 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology 70, 596–606.

Davoren, G.K., Montevecchi, W.A., Anderson, J.T., 2003. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecological Monographs 73, 463–481.

Etnoyer, P., Canny, D., Mate, B., Morgan, L., 2004. Persistent pelagic habitats in the Baja California to Bering Sea (B2B) ecoregion. Oceanography 17, 90–101.

Fauchald, P., Erikstad, K.E., Skarsfjord, H., 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81, 773–783.

Gende, S.M., Sigler, M.F., in press. Predictability of prey of Steller sea lions at varying spatial scales. Proceedings of the Wakefiled Symposium: Sea lions of the World. Alaska Sea Grant.

Grand, T.C., Grant, J.W., 1994. Spatial predictability of food influences its monopolization and defense by juvenile convict cichlids. Animal Behaviour 47, 91–100.

Guinet, C., Dubroca, L., Lea, M.A., Goldsworthy, S., Cherel, Y., Duhamel, G., Bonadonna, F., Donnay, J., 2001. Spatial distribution of foraging in female Antarctic fur seals Arctocephalus gazelle in relation to oceanographic variables: a scale-dependent approach using geographic information systems. Marine Ecology Progress Series 219, 251–264.

Haegele, C.W., Schweigert, J.F., 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Canadian Journal of Fisheries and Aquatic Sciences (Suppl 1), 39–55.

Huse, I.J., Ostrowski, M., 1998. Variation in acoustically measured abundance from repeated surveys of an isolated herring population. Journal of the Acoustical Society of America 103, 3000.

Huse, I., Korneliussen, R., 2000. Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.). ICES Journal of Marine Science 57, 903–910.

Irons, D.B., 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79, 647–655.

Kacelnick, A., Houston, A.I., 1984. Some effects of energy costs on foraging strategies. Animal Behaviour 32, 609–614.

Kacelnik, A., Krebs, J.R., 1985. Learning to exploit patchily distributed food. In: Sibly, R.M., Smith, R.H. (Eds.), Behavioural Ecology: Ecological Consequences of Adaptive Behaviours. Oxford, Blackwell Scientific Publications, Cambridge, pp. 189–205.

Kamil, A.C., 1983. Optimal foraging and the psychology of learning. American Zoologist 23, 291–302.

Kenney, R.D., Mayo, C.A., Winn, H.E., 2001. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. Journal of Cetacean Research and Management 2, 251–260.

Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., Houser, D.S., 2000. Foraging ecology of northern elephant seals. Ecological Monographs 70, 353–382.

MacLennan, D.N., Simmonds, E.J., 1992. Fisheries Acoustics. Chapman & Hall, London.

Marston, B.H., Willson, M.F., Gende, S.M., 2002. Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs. Marine Ecology Progress Series 231, 229–236.

Milinski, M., 1994. Long-term memory for food patches and implications for ideal free distributions in sticklebacks. Ecology 75, 1150–1156.

Noda, M., Gushima, K., Kakuda, S., 1994. Local prey search based on spatial memory and expectation in the planktivorous reef fish, *Chromis chrysurus* (Pomacentridae). Animal Behavior 47, 1413–1422.

Olsen, K., Angell, J., Pettersen, F., Lovik, A., 1983. Observed fish reactions to a surveying vessel with special reference to herring, cod, capelin, and polar cod. FAO Fisheries Report 300, 131–139.

Ona, E., 2003. An expanded target-strength relationship for herring. ICES Journal Marine Science 60, 493–499.

Sagar, P.M., Weimerskirch, H., 1996. Satellite tracking of southern Buller's albatrosses from the Snares, New Zealand. Condor 98, 649–652.

Siems, D.P., Sikes, R.S., 1998. Tradeoffs between growth and reproduction in response to temporal variation in food supply. Environmental Biology of Fishes 53, 319–329.

Sih, A., Christensen, B., 2001. Optimal diet theory: when does it work, and why does it fail? Animal Behaviour 61, 379–390.

Sinclair, E.H., Zepplin, T.K., 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). Journal of Mammalogy 83, 973–990.

Skov, H., Durinck, J., Andell, P., 2000. Associations between wintering avian predators and schooling fish in the Skagerrak-Kattegat suggest reliance on predictable aggregations of herring *Clupea harengus*. Journal of Avian Biology 31, 135–143.

Traynor, J.J., 1996. Target-strength measurements for walleye pollock (*Theragra chalcogramma*) and Pacific whiting (*Merluccius productus*). ICES Journal of Marine Science 53, 253–258.

3?tlsb = -0.02w? > Vollenweider, J.J., Heintz, R., in press. Seasonal variation in the whole-body energy content and proximate composition of forage fish in southeastern Alaska. Marine Ecology Progress Series.

Webb, D.G., Marcotte, B.M., 1984. Resource predictability and reproductive strategy in *Tisbe Cucumariae* Humes (Copepoda: Harpacticoida). Journal of Experimental Marine Biology and Ecology 77, 1–10.

Weimerskirch, H., 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. Oecologia 102, 37–43.

Weimerskirch, H., Wilson, R.P., Lys, P., 1997. Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. Marine Ecology Progress Series 151, 245–254.

Womble, J.N., Sigler, M.F., in press. Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. Marine Ecology Progress Series.