

Association of foraging Steller sea lions with persistent prey hot spots in southeast Alaska

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ABSTRACT: Understanding how air-breathing marine vertebrates find and utilize prey provides insight into their foraging mechanisms and ultimately their population productivity and trends. Utilization depends on their ability to locate areas where productive foraging conditions exist. We quantified the abundance of forage fish in southeast Alaska during acoustic surveys between October and April to improve our understanding of Steller sea lion *Eumetopias jubatus* foraging behavior. Energy densities (millions kJ km⁻²) of forage fish were orders of magnitude greater between November and February due to the presence of large schools of Pacific herring *Clupea pallasii*. Herring schools were highly aggregated, although the location of these aggregations shifted southward from November to April. Thus, a productive foraging area in one month did not necessarily equate to a productive area in the next month. However, by surveying on successive days and weeks, we found that herring aggregations persisted at shorter time scales. When the study area was partitioned into 1 × 1 km blocks, the day-to-day abundance of prey within a block was highly correlated with prey abundance the following day (correlation coefficient, $r = 0.75$, $p < 0.001$) and with prey abundance for the following week ($r = 0.55$, $p < 0.001$). More importantly, the persistence of these prey hot spots was an important characteristic in determining whether foraging sea lions utilized them. The odds of observing a foraging sea lion were about 1 in 3 for locations where prey hot spots were persistent. The persistence of these hot spots allowed predators to predict their locations and concentrate search efforts accordingly.

KEY WORDS: Steller sea lions · Herring · Hot spot persistence · Foraging effort

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INTRODUCTION

The ability to predict the location of prey is an important component of predator foraging behavior (Webb & Marcotte 1984, Hunt et al. 1992, Grand & Grant 1994, Siems & Sikes 1998). Nowhere is this more relevant than for air-breathing vertebrates that forage at sea. Foraging marine mammals and seabirds are faced with physiological and energetic constraints in acquiring prey that may be ephemerally available in time and patchily distributed in 3 dimensions, so predictable distributions of prey allow them to concentrate search efforts, facilitating efficient foraging (Irons 1998, Davoren et al. 2003). For marine mammals

and diving seabirds, foraging occurs by swimming through the water column visually searching for food, which is an energetically expensive activity (Costa et al. 1989, Reilly & Fedak 1991, Castellini et al. 1992).

When an area is located that is sufficiently profitable, predators will remember the location (e.g. Kacelnik & Krebs 1985, Milinski 1994, Irons 1998), and concentrate their search efforts accordingly (i.e. long-term area-concentrated search; Bell 1991, Bonadonna et al. 2001). This behavior is adaptive because foraging efficiency is often strongly linked to fitness, particularly when foraging distance is spatially constrained. For example, many pinnipeds and seabirds must return to rookeries or breeding colonies on a

regular basis to rest and feed offspring. The inability to find productive foraging areas efficiently may result in starvation of offspring (Costa et al. 1989), brood reduction (Braun & Hunt 1983), or abandonment by incubating adults (Weimerskirch 1995, Arnold et al. 2004). When individuals can anticipate the distribution of prey and concentrate their efforts at these sites, they can reduce costly unsuccessful search effort (Grand & Grant 1994, Cuthill et al. 2000) and time spent exposed to predators (Lima 1986).

One mechanism that can contribute to the ability of predators to efficiently find prey is the persistence of profitable foraging patches through time. Here, predators learn these locations (Kamil 1983, Alonso et al. 1995) and base their search efforts on spatial memory and the expectation of productive foraging (e.g. Noda et al. 1994). Persistence may occur at short time scales, allowing predators to predict the location of prey during consecutive foraging bouts (e.g. Bonadonna et al. 2001), or at longer time scales, such that seasonal migrations are directed around profitable foraging areas (Marston et al. 2002, Sigler et al. 2004, 2009, Womble et al. 2009).

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 (e.g. Le Boeuf et al. 2000, Guinet et al. 2001, Sinclair & Zeppelin 2002) and seabirds (e.g. Skov et al. 2000), very few studies have quantified prey persistence for marine predators (Davoren et al. 2003, Davoren 2013). Previously, we examined the monthly spatial distribution of forage fish in southeast Alaska to better understand Steller sea lion *Eumetopias jubatus* foraging behavior (Gende & Sigler 2006, Womble & Sigler 2006, Sigler & Csepp 2007). Steller sea lions utilize seasonally abundant and densely aggregated prey (Sinclair & Zeppelin 2002, Sigler et al. 2004, 2009, Womble & Sigler 2006) because foraging efficiency declines when prey are less dense (Goundie et al. 2015) and diet quality can affect body condition (Rosen & Trites 2005, Jeanniard du Dot et al. 2008).

As part of our previous efforts, we found that during winter, large aggregations of herring, which were the most common prey species in sea lion diet (frequency of occurrence, FO = 90%) and comprised over 81% of the available pelagic prey biomass during pelagic surveys (Womble & Sigler 2006), consistently occurred in a few areas in Lynn Canal (southeast Alaska; Sigler & Csepp 2007). Moreover, these prey 'hot spots' persisted through winter and were located in the same areas across years (Gende & Sigler 2006). We also found that over 40% of the vari-

ation in monthly distributions of sea lions occupying a nearby terrestrial haulout was explained by the persistence of these herring hot spots (Gende & Sigler 2006). In contrast, there was no relationship between the biomass of walleye pollock *Gadus chalcogrammus* (which are also an important diet item for sea lions; FO = 88%) and the distribution of foraging sea lions.

While these studies provided evidence that sea lions can target certain foraging areas from one month to the next, sea lions typically embark on foraging trips on a daily or weekly basis, depending on season, age, sex, and reproductive status (Merrick & Loughlin 1997, Loughlin et al. 2003, Fadely et al. 2005, Call et al. 2007). We wanted to understand the characteristics of prey on a day-to-day and weekly basis and their influence on sea lion foraging locations. We thus designed the present study to quantify, using acoustic survey methods, the daily distributions of forage fish in pelagic environments of southeast Alaska while simultaneously collecting data on the distribution of Steller sea lions. Our goal was to improve understanding of how the spatial and temporal dynamics of prey influence the foraging ecology and behavior of the predators that utilize them. Specifically, we quantified (1) the daily distributions of pelagic forage fish and where prey hot spots occurred; (2) whether these hot spots persisted at daily or weekly time scales; and (3) the location of foraging sea lions relative to hot spot persistence.

MATERIALS AND METHODS

Study area

Acoustic surveys were conducted in Favorite Channel, southeast Alaska, between Outer Point (58° 16' N, 134° 42' W) and Benjamin Island (58° 36' N, 134° 56' W) between October 2004 and April 2005 (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 southeast Alaska. It also includes a site (Benjamin Island) used as a seasonal haulout, where up to 600 sea lions are present from October until April (Womble & Sigler 2006). This area encompasses a submarine gully that extends nearly continuously within our study area and is oriented north-south with a branch extending eastward into Fritz Cove. The water depth of the bottom of the

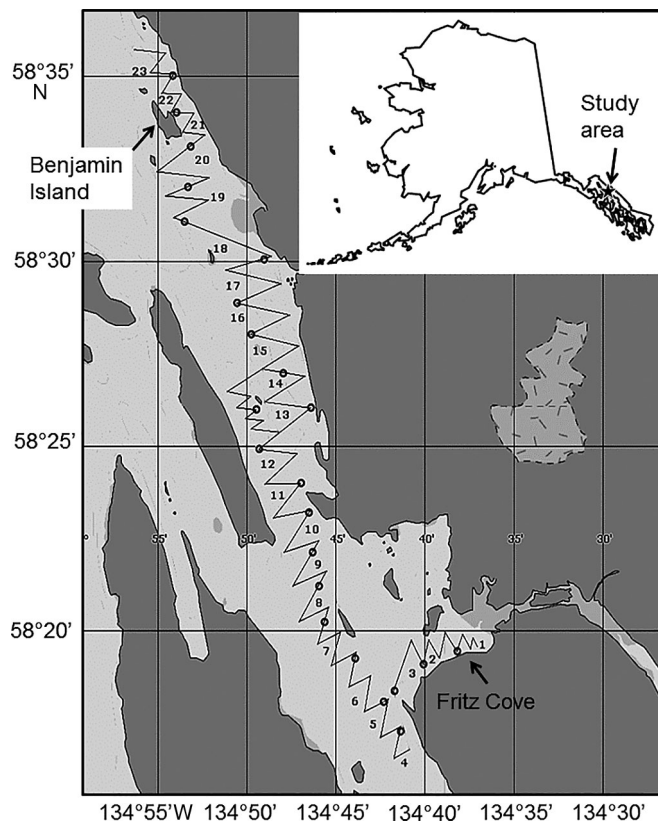


Fig. 1. Location of acoustic and Steller sea lion surveys in upper Lynn Canal, southeastern Alaska. Open circles: boundary of the survey blocks, which are numbered. This area encompasses a submarine gully (blocks 4 to 23) that extends nearly continuously within our study area and is oriented north-south with a branch extending eastward into Fritz Cove (blocks 1 to 3)

gully ranges from 80 to 130 m. Herring were found in the submarine gully each winter during the 3 yr of our previous study (Gende & Sigler 2006, Sigler & Csepp 2007) and have appeared there over a 3 decade span, although the distribution center has shifted somewhat (Sigler & Csepp 2007).

Up to 5 surveys were conducted each month. The first 4 surveys were conducted on successive days and the fifth was conducted 1 wk after the first (e.g. Monday, Tuesday, Wednesday, Thursday and the following Monday). This timing was chosen so that spatial patterns of abundance could be compared between successive days (e.g. Monday and Tuesday) and between successive weeks (e.g. Monday and the following Monday). Each set of (up to) 5 surveys were labeled by month (e.g. the 5 surveys completed during 10 to 17 November 2004 were termed the 'November surveys'). Occasionally, bad weather prevented the completion of all 5 surveys planned within a month.

Data collection

To quantify pelagic fish distributions, we used a portable 38 kHz Simrad EK60 split-beam echo-integration system with a 12° beam angle, towed at 11 km h⁻¹ from the FV 'Sea View'. The echo-integration system was periodically calibrated with a standard 60 mm copper sphere of known acoustic density (MacLennan & Simmonds 1992). Simultaneously, an observer stationed on the bridge of the acoustic survey vessel used Nikon 7 × 50 binoculars to scan for sea lions in the water along the transect route (Fig. 1). The location and activity (foraging, milling, or traveling) of any observed sea lion was recorded. Sea lions were recorded as foraging if they were observed consistently diving in an area, traveling if they were seen swimming at or near the surface in a consistent direction, and milling if seen on the surface but not diving. Location data were collected using a Garmin global positioning system with location accuracy of 10 m or less.

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 & Korneliussen 2000), thereby changing the distribution and density estimates. However, we chose to sample during daylight hours (between 08:00 and 17:00 h) because it facilitated observations of foraging sea lions during collection of acoustic data. Daytime acoustic surveys also minimize the potential for vessel avoidance by species near the surface, which for herring—which are deeper during the day—may be substantial (Olsen et al. 1983, Huse & 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 errors across all sampling periods, thereby minimizing the impacts on our results (Huse & Korneliussen 2000). Finally, although sea lions forage at night, they also commonly forage during the day (Merrick & Loughlin 1997, Pitcher et al. 2005), and thus we felt that it was reasonable to relate characteristics of prey distributions relative to sea lion distributions during daylight hours.

Length, weight, and species classification data, necessary complements to acoustic data, were collected quarterly with a midwater trawl deployed from the 37 m RV 'Medeia' in December 2004 and March 2005. The mid-water trawl was 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 0.185 km length

intervals (0.1 nautical mile, nmi) and 10 m depth intervals, and corrected for instrument calibration using the echo-integration software SonarData Echoview (Echoview Software 2015; <https://www.echoview.com/>). To convert the acoustic backscatter (nautical area scattering coefficient [NASC]; $\text{m}^2 \text{nmi}^{-2}$) (MacLennan et al. 2002) to fish density in numbers, acoustic reflectivity for single fish was estimated using length- and species-specific target strength (TS, dB re 1 m^2) (MacLennan et al. 2002) equations of the generalized form: $\text{TS} = 20 \log_{10} L + b$ (MacLennan & Simmonds 1992). In this equation, L is fish length in cm and b is a species-specific coefficient, where $b = -66$ for walleye pollock (Traynor 1996) and $b = -65.4$ for Pacific herring (Ona 2003). NASC and TS values for herring were further adjusted for acoustic shadowing and depth compression of the air bladder (Ona 2003, Sigler & Csepp 2007). TS values were transformed to backscattering cross-section, $\sigma_{\text{bs}} = 4\pi 10^{\text{TS}/10}$ 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 (Schaufler et al. 2006). We present results of prey in terms of energy as a common 'currency' for foraging decisions (Kacelnik & Krebs 1985). Whereas variability in mass-specific energy content between individual herring and walleye pollock was approximately 2-fold (8.5 vs. 4.8 kJ g^{-1} , respectively; see Schaufler et al. 2006), 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, biomass and energy estimates were highly correlated (pollock: $r^2 = 0.99$; herring $r^2 = 0.98$), and thus we report results only in terms of nutritional energy. Nutritional energy is expressed in density units of millions of kJ km^{-2} by species, 0.185 km transect, and 10 m depth interval.

Data analysis

Each 10 m depth interval within its corresponding 0.185 km transect was 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 study area was then partitioned into spatial blocks, where each block

encompassed a latitudinal minute (e.g. $58^\circ 25'$ to $58^\circ 26'$ N, a distance of 1.83 km). In Fritz Cove, which is oriented east–west, each block encompassed 2 longitudinal minutes, which is approximately the same distance as one latitudinal minute at this latitude. We then computed the estimated energy density for each block by averaging all the (depth-integrated) 0.185 km transects that fell within that block (each block contained at least 11 transects). The study area thus consisted of 23 latitudinal blocks, each with an estimated energy density for each day surveyed. The block is the spatial scale at which we conducted our analyses.

As we were interested in evaluating how foraging sea lions may be spatially associated with prey hot spots (Davoren 2013, Volkenandt et al. 2016), we designated each block as 'hot' or not (i.e. 'cold'). A block was defined as hot if it supported greater than average prey energy densities, where the average was calculated for all blocks within that day (see similar procedures in Davoren et al. 2003). In this method, hot spots are defined based on their energy density relative to the other blocks that day. This method results in a day-specific binary designation of each block as hot or not. As blocks were surveyed for 5 d over an 8 d period (which we term a 'week'), each block could be hot for up to a maximum of 5 d. Persistence of hot spots (blocks) was calculated for each week by summing the number of days that block was hot divided by the total number of days it was surveyed. For example, if a block was above average for 2 of 5 d, then persistence for the week was 0.4. Note that we use the term 'blocks' synonymously with 'spot', so that our analysis is examining hot spot (or block) persistence.

We then compared locations of foraging Steller sea lions to the locations of persistent hot spots. From the data on the location and activity (foraging, milling, and traveling) of any observed sea lion, we labeled whether each block contained a foraging sea lion or not. We used logistic regression (Hosmer & Lemeshow 2000) to explore the relationship between the presence of foraging sea lions and both average prey energy density and the persistence of prey hot spots. Logistic regression analysis tested if the presence of a foraging sea lion at a block was more likely when prey energy density was high that day or prey energy density was consistently high that week (i.e. a persistent hot spot): $\text{logit}(Y_{ij}) = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ik} + \epsilon_{ij}$, where i represents a block, j represents a day, and k represents a week; Y_{ij} is the ij^{th} observation of presence or absence of a foraging sea lion (value of 1 or 0, respectively), X_{1ij} is the log-transformed prey energy density for that day (natural log transform of prey

energy density + 1, i.e. $X_{1ij} > 0$), X_{2ik} is the persistence value for that week (value from 0 to 1) and ϵ_{ij} is the error term. Although this analysis considered only foraging sea lions, most (80%) of the sea lions seen were classified as foraging and thus results only changed slightly if we included sea lions from all behavioral categories.

We used generalized additive model (GAM) regression to test for correlation between adjacent blocks (Wood 2006), i.e. $\epsilon_{ij} = \phi\epsilon_{i-1,j} + \epsilon_{ij}$ for the equation in the previous paragraph. The blocks form a line (Fig. 1; apart from the minor exception that block 3 is adjacent to block 5 rather than block 4) and thus measurements between adjacent blocks may be correlated. The smooth functions for prey energy and prey persistence were constrained to biologically realistic forms (maximum of 3 degrees of freedom allowing for linear, dome-shaped, asymptotic, and sigmoidal relationships). The estimated value of ϕ was small (0.15) and predicted values and their 95% CI were similar with and without autocorrelation. Thus, final models did not include autocorrelation.

We compiled FO for persistence values by month (e.g. the number of blocks with persistence = 1 during November). We also compiled the FO of foraging sea lions (present, absent) which we compared to persistence values for all months combined (e.g. the proportion of blocks with foraging sea lions observed for persistence = 1). For this compilation, a χ^2 test was completed based on the counts to determine whether FO significantly differed between observations with and without foraging sea lions.

RESULTS

A total of 28 acoustic surveys were conducted between October 2004 and April 2005. Five surveys were conducted each month between November 2004 and March 2005 ($n = 25$ surveys), which were the focal months for examining daily persistence of prey. In addition, 2 surveys were conducted in October 2004 and 1 survey in April 2005 to measure prey abundance during months when lower prey abundance was anticipated for the study area. In February 2005, bad weather limited sampling on 2 survey days to 13 and 15 survey blocks (normally 22 or 23 survey blocks) and delayed the fifth survey until 17 d following the first survey (rather than the planned 7 d).

The energy density of pelagic prey available to foraging Steller sea lions varied among seasons. In October, the average energy density in the survey area was 131 million kJ km^{-2} , jumped to 1015 million

kJ km^{-2} in November, and remained high through February before dropping to 190 million kJ km^{-2} by March (Fig. 2). Pelagic prey increases were predominantly due to the presence of large schools of herring that moved into the area after October (energy density attributable to herring increased over 900% from October to November). Consequently, the average energy density for the winter months (November to February) exceeded the average for October, March, and April (1392 million vs. 175 million kJ km^{-2} ; 2-tailed t -test, $df = 24$, $p < 0.001$) (Fig. 2).

Coincident with the increased energy density, the spatial distribution of prey energy density was concentrated during November to February. For example, 75% of prey energy during a given day was distributed across an average of 5 blocks in October, but only 1 block in November, 2 blocks in December, and 3 blocks in January. In March, prey started to dissipate, and by April, this average had increased to 6 blocks.

The location of the prey hot spots gradually shifted from northern to southern blocks during our study (Fig. 3). For example, prey energy densities were higher at blocks 18 to 22 during November to December but were low thereafter (Fig. 3). In contrast, prey energy densities were lower at blocks 12 to 16 during October to November but were higher during December to February.

Hot spot persistence

Hot spots of prey generally persisted on a daily basis. For example, 3 to 7 of the 23 blocks were hot on all sampled days within a week (persistence = 1)

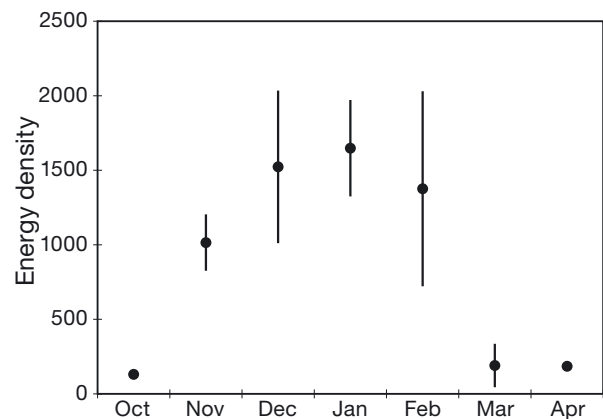


Fig. 2. Average monthly values of prey energy density (million kJ km^{-2}) in upper Lynn Canal, southeastern Alaska, during October 2004 to April 2005. Vertical lines: 90% CI for the average (\bullet). A confidence interval could not be computed for April 2005 because only 1 survey was conducted that month

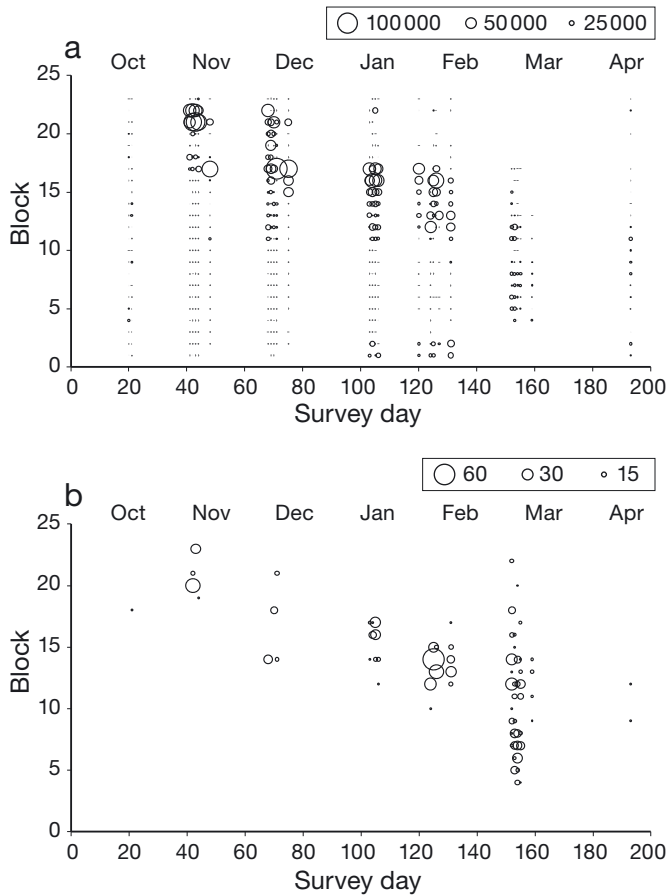


Fig. 3. (a) Temporal and spatial distribution of prey energy in upper Lynn Canal, southeastern Alaska, during October 2004 to April 2005. Each data point represents the density of nutritional energy (millions of kJ km^{-2}) for a survey block and day (the area of the circle is proportional to nutritional energy). (b) Spatial distribution of foraging sea lions in upper Lynn Canal, southeastern Alaska, during October 2004–April 2005. Each data point represents the number of foraging sea lions for a survey block and day (the area of the circle is proportional to the number of foraging sea lions)

Table 1. Number of blocks within selected persistence ranges tallied by month: consistently hot (persistence = 1); mostly hot (persistence 0.75 to 1); consistently cold (persistence = 0). Values of prey persistence of nutritional energy (millions of kJ km^{-2}) for a survey block and month in upper Lynn Canal, southeastern Alaska, during November 2004 to March 2005. Persistence is defined as the proportion of survey days that prey energy at a block is above average that day. Only months with 5 surveys are presented, which excludes October 2004 (2 surveys) and April 2005 (1 survey)

Persistence range	Nov	Dec	Jan	Feb	Mar
1	3	3	6	4	7
0.75–1	5	9	7	6	8
0	11	11	12	9	11

(Table 1). Between 5 and 9 blocks were hot on most sampled days within a week (persistence ≥ 0.75). Prey abundance often was consistently cold at blocks within a month (9 to 12 blocks with persistence = 0, which implies lower prey abundance on all survey days for these blocks). Thus, knowledge of the locations of hot and cold blocks has the potential to reduce foraging costs for predators because many blocks had consistent patterns of prey abundance. Of the 23 blocks usually sampled each survey day, at least two-thirds were consistently hot (persistence ≥ 0.75) or cold (persistence = 0) each month (Table 1).

While the locations of hot and cold blocks were predictable on daily and weekly bases (correlation, natural log transform of prey energy density + 1), the explanatory power diminished as the time interval lengthened. Prey abundance at a block was correlated with prey abundance for the following day ($r = 0.75$, $p < 0.001$) and with prey abundance for the following week ($r = 0.55$, $p < 0.001$). This predictability reflected specific locations of pelagic prey hot spots. For example, between November and February, northerly blocks 14 to 17 (December to February) and 21 to 22 (November to December) were consistently characterized by large schools of herring (Fig. 4) whereas herring schools were consistently absent from the southern part of our study area during these months. Several spots either were never hot or were hot only occasionally, resulting in

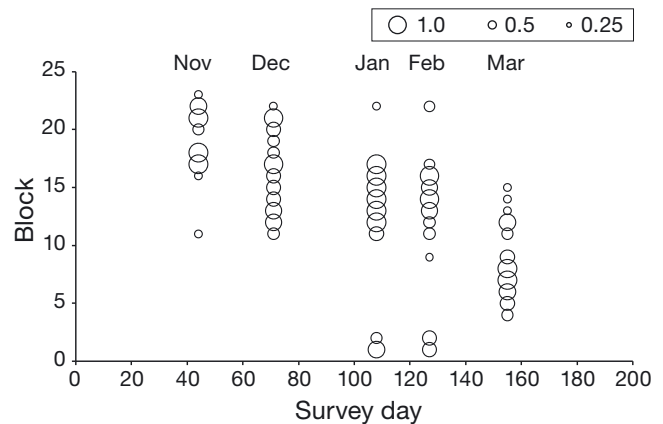


Fig. 4. Temporal and spatial distribution of prey persistence in upper Lynn Canal, southeastern Alaska, during November 2004 to March 2005. Each data point represents the persistence of nutritional energy (millions of kJ km^{-2}) for a survey block for 1 wk during each month. Persistence is defined as the proportion of survey days that prey energy at a block is above average that day (the area of the circle is proportional to the persistence value). Only months with 5 surveys are presented (November 2004 to March 2005), which excludes October 2004 (2 surveys) and April 2005 (1 survey)

low persistence. Eventually, during March when herring spread further southward, a few southerly blocks (e.g. 5 to 8) were consistently hot. Before March, prey energy in blocks 5 to 8 had never been hot.

Relationship between sea lion distribution and hot spot persistence

During acoustic surveys, a total of 711 sea lions were recorded during 87 observations. Group size varied from 1 to 64. 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). Sightings were more common during March than other months (Fig. 3). Sightings were more frequent in northerly blocks in November and shifted southward in the following months, similar to the pattern for pelagic prey energy (Fig. 3).

Prey energy density influenced how often foraging sea lions were observed. Foraging sea lions were observed more often where prey energy density was consistently hot ($\chi^2 = 31.2$, $df = 8$, $p < 0.001$). Of the survey blocks with foraging sea lions, many (0.62) were consistently hot (prey persistence ≥ 0.75); compared to blocks without foraging sea lions, only few (0.17 of blocks) were consistently hot (Table 2). In contrast, of the survey blocks without foraging sea lions, many (0.59) were consistently cold (persistence = 0); compared to blocks with foraging sea lions, few (0.18) were consistently cold.

During November to March, persistence was a better predictor of sea lion presence than average density. During these months, there was a strong

Table 2. Proportion of survey blocks within selected persistence ranges tallied by presence or absence of foraging Steller sea lions: consistently hot (persistence = 1); mostly hot (persistence 0.75–1); consistently cold (persistence = 0). Values of prey persistence of nutritional energy (millions of kJ km^{-2}) for a survey block and month in upper Lynn Canal, southeastern Alaska, during November 2004 to March 2005. Persistence is defined as the proportion of survey days that prey energy at a block is above average that day

Persistence range	No foraging sea lions	Foraging sea lions
1	0.09	0.47
0.75–1	0.17	0.62
0	0.59	0.18

relationship between the probability of observing a foraging sea lion and the persistence of hot spots. At these hot spots, we often observed sea lions diving on the herring schools. While foraging location appears to be influenced by whether prey were abundant that day, the logistic regression relationship was not statistically significant ($\beta_1 = -0.105$, $SE = 0.067$, $p = 0.119$). The negative β_1 value is contrary to expectation; however, the magnitude is small and not significantly different from zero. Foraging appears to be influenced by whether prey hot spots were persistent; in this case, the relationship is statistically significant ($\beta_2 = 3.44$, $SE = 0.557$, $p < 0.001$). To evaluate goodness-of-fit of the logistic model, we computed McFadden's pseudo- R^2 ; the value for the full model was 0.180. The hot spot persistence parameters also were estimated for the reduced model ($\beta_2 = 2.84$, $SE = 0.387$, $p < 0.001$). The value of McFadden's pseudo- R^2 for the reduced model was 0.174. The positive β_2 value implies that sea lions are observed more often when hot spots are persistent. Based on the logistic regression, the estimated odds of observing a foraging sea lion were higher at locations where prey concentrations persisted (Fig. 5). For example, the odds of observing a foraging sea lion at a block that was consistently cold were about 1 in 20, whereas for a block that was consistently hot, the odds were about 1 in 3 (Fig. 5).

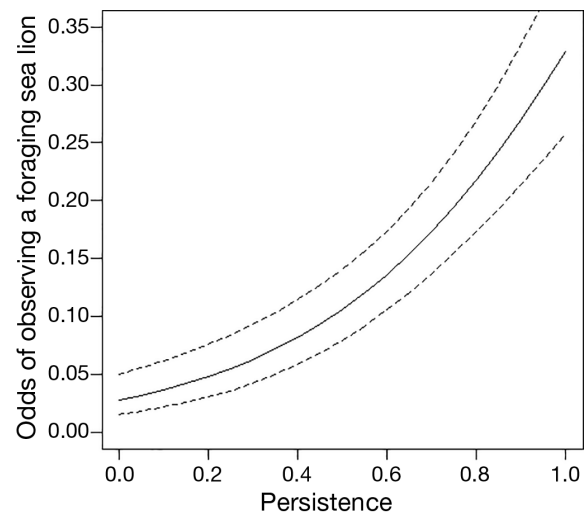


Fig. 5. The odds of observing a foraging sea lion in upper Lynn Canal, southeastern Alaska, during October 2004 to April 2005 as a function of prey persistence (solid line; dashed lines: 2.5 and 97.5% CI). Persistence is defined as the proportion of survey days that prey energy at a block is above average that day

DISCUSSION

Dynamics of pelagic prey for Steller sea lions

Our study demonstrated 2 important attributes of the pelagic prey relevant to sea lion foraging decisions in southeast Alaska. First, prey distributions were heterogeneous, with a relatively small number of areas constituting a large fraction of the available prey biomass and energy. This produced a patchwork of prey hot spots (and cold spots) across the study area between November and March. Second, these prey hot spots persisted from day to day, and generally persisted among weeks, allowing sea lions to use information on the location of profitable foraging areas to target search efforts for near-future foraging trips.

Both of these attributes were a function of the life history and behavior of Pacific herring, which constituted almost all of the available prey energy during our study. In November, large schools of herring moved into the study area accounting for the orders of magnitude difference in pelagic prey energy from October to November. We highlight that the average energy density quantified during this study was similar to previous years (Gende & Sigler 2006), demonstrating that herring typically utilize the same overwintering areas on an annual basis. Throughout the winter, herring typically do not feed because their primary prey, copepods, are at very low abundances. Consequently, individual herring tend to follow an energy conservation strategy by minimizing movements (Corten 2002, Ona 2003). This is why the foraging hot spots persisted at shorter time scales. By March, herring begin to migrate en masse to spawning areas (Carlson 1980), after which they subdivide into smaller foraging schools and disperse (Haegle & Schweigert 1985), generally moving much more extensively in pursuit of ephemeral patches of copepods.

Many studies have documented that marine mammals (e.g. Bonadonna et al. 2001, Guinet et al. 2001) and seabirds (e.g. Sagar & Weimerskirch 1996, Hunt et al. 1998, Irons 1998) regularly commute to preferred foraging areas, and will use previous knowledge to help relocate these areas (e.g. Kenney et al. 2001). However, our results were insightful because sea lions were associated with prey hot spots that had the highest persistence, rather than aggregating at the spots that supported the highest abundance on that day. Similarly, Decker & Hunt (1996) inferred that foraging murre near the Pribilof Islands concentrated at oceanographic fronts, even when areas out-

side the fronts supported high concentrations of prey, because prey could be located more predictably within the frontal zones.

In an earlier study (Gende & Sigler 2006), we demonstrated, using a simple 2-dimensional spatial model, that sea lion foraging efficiency was markedly improved 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 did not negate their value because it took sea lions little effort to find these locations once in the area where prey persisted. In our study area, individual sea lions appear to return to the nearby haulout, Benjamin Island, between foraging bouts because we never observed floating rafts of sea lions resting at the surface above areas where herring schools were located. Thus, unlike other pinnipeds such as Northern elephant seals, which may remain at sea for months (Stewart & DeLong 1995), daily persistence of prey hot spots has tremendous value for sea lions because they must make repeated decisions throughout the winter on where to concentrate daily or weekly search efforts. In addition to reducing the energy expended during search efforts, knowing the likely locations of profitable foraging areas also reduces their exposure to predators such as killer whales *Orcinus orca* and, possibly, sleeper sharks *Somniosus pacificus* (Horning & Mellish 2014).

Steller sea lions benefit from densely aggregated (Sinclair & Zeppelin 2002, Sigler et al. 2004, 2009, Womble & Sigler 2006) and persistent (Gende & Sigler 2006, this study) prey. In southeast Alaska, sea lion numbers are increasing (Pitcher et al. 2007, NMFS 2013, Fritz et al. 2016) and their winter foraging often focuses on herring; outside winter, other seasonally aggregated prey (e.g. walleye pollock, Pacific salmon *Oncorhynchus* spp., sand lance *Ammodytes hexapterus*) are important (Sigler et al. 2004, 2009, Womble & Sigler 2006, Trites et al. 2007). In the western Aleutians, sea lion numbers are decreasing (Johnson & Fritz 2014, Fritz et al. 2016) and sea lions also rely on densely aggregated prey such as Atka mackerel *Pleurogrammus monopterygius*, Pacific cod *Gadus macrocephalus*, Pacific salmon, and walleye pollock, particularly when they are aggregated to spawn (Sinclair & Zeppelin 2002, Sinclair et al. 2013). The studies from southeast Alaska imply that these aggregations benefit Steller sea lions, with the amount of benefit depending on aggregation density and persistence.

Alternative definition of hot spot

For our study, we portioned the total area into spatial blocks, and assigned that block as 'hot' if prey energy density was above average for that day (see similar procedures in Davoren et al. 2003). However, we recognize that there may be some prey thresholds above or below which the absolute abundance of prey in an area makes it unprofitable (even if it is above average for that day) or of limited profitability (if it is superabundant). To explore this idea, we derived an alternative metric of persistence based on a fixed threshold, where the threshold was defined based on the average energy density of blocks where sea lions were observed foraging. During the study, prey energy density was significantly higher in blocks where sea lions were observed foraging ($\bar{x} = 745$ million kJ km⁻²; threshold) compared to all blocks where no sea lions were present ($\bar{x} = 92$ million kJ km⁻²) (log-normal error, 2-tailed *t*-test, $p < 0.001$). Thus, any block with more than 745 million kJ km⁻² was considered hot. While this threshold definition was somewhat arbitrary, the results for the 2 methods were largely similar. Like the daily average method for defining a hot spot, persistence explained a significant amount of the variation in sea lion presence using this threshold method ($\beta_2 = 2.16$, SE = 0.554, $p < 0.001$). Likewise, the odds of observing a foraging sea lion at a block that was consistently cold were about 1 in 20, whereas for a block that was consistently hot, the odds were about 1 in 3 regardless of which method was used to define persistence. We thus conclude that persistence is the important attribute rather than the method of defining a hot spot.

We also recognize some limitations by defining prey abundances using a standard block size rather than characterizing each prey patch individually. Individual prey patch characteristics such as local density and depth may better predict habitat use by predators than overall prey abundance (Benoit-Bird et al. 2013). However, our block scale was smaller than the sizes of most prey aggregations (Fig. 3), so that local densities were not masked by large block sizes. In addition, local density and depth were fairly homogeneous, with dense herring aggregations located near the seafloor at similar depths, so that contrasts in these prey characteristics were small and unlikely to influence our results.

CONCLUSIONS

Many studies have examined movements and habitat use by foraging seabirds and marine mam-

mals but with little to no information on the density and movements of their prey. Other studies have examined the density and distribution of forage fish and lower trophic level aggregations but with little information on their predators. Our study combines these 2 disciplines. Combining information on both prey and predators allowed us to infer that hot spot persistence is an important attribute 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 (e.g. Sigler et al. 2012), to test the applicability of these results.

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