

Movements of wintering surf scoters: predator responses to different prey landscapes

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Abstract The distribution of predators is widely recognized to be intimately linked to the distribution of their prey. Foraging theory suggests that predators will modify their behaviors, including movements, to optimize net energy intake when faced with variation in prey attributes or abundance. While many studies have documented changes in movement patterns of animals in response to temporal changes in food, very few have contrasted movements of a single predator species naturally occurring in dramatically different prey landscapes. We documented variation in the winter movements, foraging range size, site fidelity, and distribution patterns of a molluscivorous sea duck, the surf scoter (*Melanitta perspicillata*), in two areas of coastal British Columbia with very different shellfish prey features. Baynes Sound has extensive tidal flats with abundant clams, which are high-quality and temporally

stable prey for scoters. Malaspina Inlet is a rocky fjord-like inlet where scoters consume mussels that are superabundant and easily accessible in some patches but are heavily depleted over the course of winter. We used radio telemetry to track surf scoter movements in both areas and found that in the clam habitats of Baynes Sound, surf scoters exhibited limited movement, small winter ranges, strong foraging site fidelity, and very consistent distribution patterns. By contrast, in mussel habitats in the Malaspina Inlet, surf scoters displayed more movement, larger ranges, little fidelity to specific foraging sites, and more variable distribution patterns. We conclude that features associated with the different prey types, particularly the higher depletion rates of mussels, strongly influenced seasonal space use patterns. These findings are consistent with foraging theory and confirm that predator behavior, specifically movements, is environmentally mediated.

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Introduction

Documenting how animal movements vary in relation to environmental factors, particularly the abundance, quality, and distribution of prey, can lead to important ecological insight. For example, animal movement patterns have been used to infer habitat quality (Winker et al. 1995), estimate minimum space requirements (Mitchell and Powell 2004), and evaluate flexibility of individuals to habitat change (Macdonald and Rushton 2003). Studies of animal movement can also reveal the mechanisms underlying foraging strategies and animal distributions (Pyke 1983). These insights are based on a growing body of knowledge

addressing the behavioral and functional relationships between predators and their prey, which in turn have direct implications for conservation and management of species and their habitats.

Ideal free distribution (IFD) concepts predict that predator densities should be positively correlated with prey densities (Fretwell and Lucas 1970). Similarly, foraging theory suggests that animals behave in ways that optimize energy intake (Stephens and Krebs 1986). Accordingly, changes in the distribution of predators resulting from movements by individuals can reflect the underlying differences in the availability or quality of prey within a habitat. Prey attributes also dictate how much space a predator must use to meet its energetic requirements (i.e., its home range, McNab 1963; Harestad and Bunnell 1979). Habitats with high resource availability allow individuals to meet daily and seasonal requirements within relatively small areas (Fisher 2000; Smith and Schaefer 2002). However, if there is temporal or spatial variability in resource availability, then individuals must modify their behavior. One important implication of this environmentally mediated response by predators is modification of distributions and movements as individuals shift to occupy more profitable foraging areas when prey availability declines (Charnov et al. 1976; Pyke 1983; Stephens and Krebs 1986). Patchy spatial distribution, ephemeral availability, and rapid depletion by conspecifics have all been shown to lead to increased movement probability and larger home ranges for predators (Tufto et al. 1996; Ferguson et al. 1999).

Along with habitat and prey features, sex and age can influence movements, site fidelity, and dispersal (Greenwood 1980). Male-biased movement is common, as males often range farther in mate-searching activities (Greenwood 1980; Rohwer and Anderson 1988; Robertson and Cooke 1999). For example, pair bonding occurs in late winter for many waterfowl including sea ducks (Robertson and Cooke 1999), and unpaired males searching for females could show longer distance movements and increased overall space use. Juveniles often demonstrate increased movement and lower site fidelity (Baldassarre et al. 1988; Robertson and Cooke 1999; Cooke et al. 2000), potentially because they are unfamiliar with wintering areas or they may be excluded from optimal habitats by more dominant adult foragers.

Numerous empirical studies have described the movement responses of animals to temporal changes in prey distribution, abundance, or quality (Van Eerden 1984; Einarsson 1988; Tufto et al. 1996; Warnock and Takekawa 1996; Marzluff et al. 1997; Ferguson et al. 1999). However, few studies have had the data to evaluate the movement behavior of a single species in dissimilar foraging landscapes using multiple data sources. We evaluate movements, home range size, site fidelity, and distributional

consistency of a molluscivorous sea duck, the surf scoter (*Melanitta perspicillata*), which winters in two distinct habitats on the Pacific coast of North America: soft-bottomed intertidal flats where clams are the primary prey and rocky intertidal shores where mussels dominate the diet. There are important differences in attributes of clams and mussels as prey for surf scoters. In general, clams are widely distributed, with variation in density occurring in relation to specific habitat features, particularly sediment type and tidal height (Byers 2002). Unlike mussels, which are epibenthic, clams are buried in the sediment and require excavation by scoters. Clams also occur in much lower densities than mussels, which grow in dense visible clusters on hard surfaces (Fig. 1). Therefore, clam foraging requires higher investment in underwater search time relative to the more

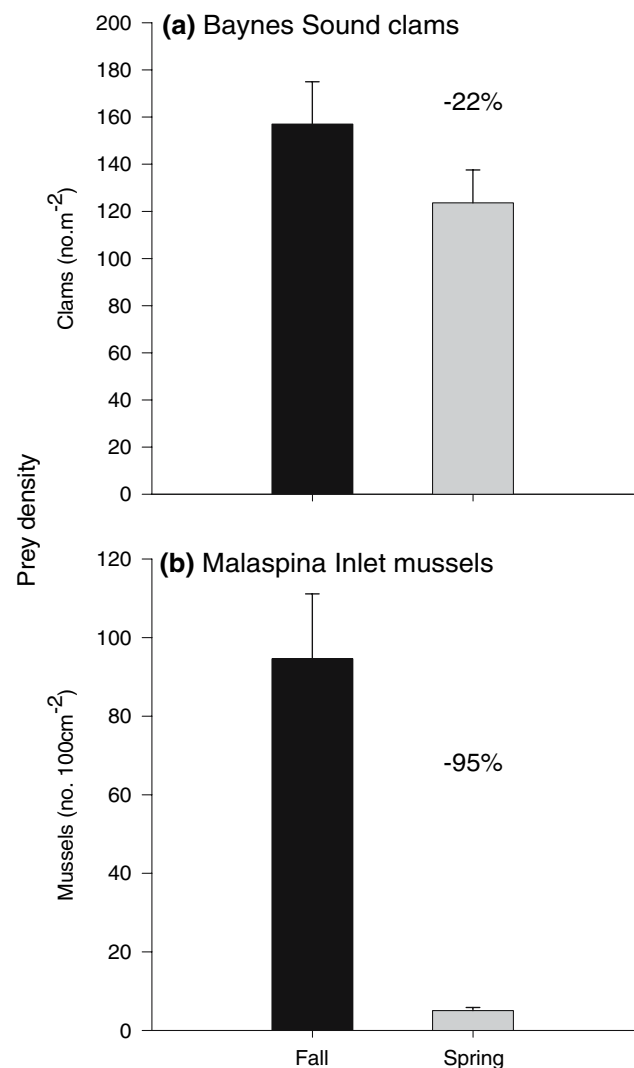


Fig. 1 Prey density (mean + 95% confidence intervals) in fall and spring for **a** Baynes Sound clams (Lewis et al. 2007) and **b** Malaspina Inlet mussels (Kirk et al. 2007). The over-winter percent change in prey density is indicated for each study area

accessible mussels, but also results in higher energetic gain. In addition to differences in the density and distribution of the two prey types is a marked disparity in depletion rates (Fig. 1). Mussels are highly available early in the winter, but patchily distributed and heavily depleted through the season, in comparison to clams, which are more temporally stable prey. Over-winter depletion of clams caused by foraging scoters is estimated to be 22% (Lewis et al. 2007), while the decrease in mussels over the winter can exceed 95% (Lacroix 2001; Kirk et al. 2007).

These factors make for an unusually well-suited natural system for evaluating environmentally mediated movements of predators, as (1) the two types of bivalve prey have very different attributes that are expected to influence foraging profitability, (2) surf scoters occur freely in both habitats, and (3) bivalve prey are spatially static and thus the prey landscape is relatively easy to quantify. In this study, we use radio-telemetry data from marked individuals in each foraging landscape along with regular surveys to test a series of hypotheses concerning surf scoter space use, movements and distributions. Three separate sets of metrics were used. First, we estimated home range size and infix distance, measured as the mean distance between consecutive observations. Second, because some sea ducks are known to exhibit strong site fidelity to specific wintering areas (Iverson and Esler 2006), we used a modified Kaplan–Meier procedure to determine the probability that a surf scoter would remain faithful to one foraging site for the entire winter period. Finally, we used a measure of distributional consistency to evaluate variation in abundance estimates at survey locations. We predicted that (1) home range size and infix distance, measured as the mean distance between consecutive individual locations, would be larger in the rocky shoreline foraging landscape (2) foraging site fidelity would be higher in the soft-bottomed intertidal foraging landscape, (3) distributional consistency, measured as the probability the distribution pattern of surveyed ducks remains constant, would be lower in the more spatially variable and easily depleted rocky shoreline foraging landscape, and (4) adult males and hatch-year birds would show increased overall levels of movement. By understanding the underlying movement decisions that lead to observed distribution patterns, we hope to identify important features of winter areas, as well as measure general habitat quality and resource use.

Material and methods

Study areas

Our research was conducted in Malaspina Inlet and Baynes Sound, two regions within the Strait of Georgia,

British Columbia, each representing a distinct foraging environment for surf scoters. Differences between the two areas are primarily related to natural habitat distinctions and to differences in the type and extent of shellfish aquaculture. Malaspina Inlet (50.0°N, 124.7°W) is composed of a series of narrow fjords on the mainland, where shellfish aquaculture activity is largely deep-water farming of oysters using floating structures. The intertidal area includes rock walls and shelves, reefs, and relatively few soft-sediment beaches. The principle prey of surf scoters in Malaspina Inlet is mussels (*Mytilus trossulus*), which occur in dense aggregations on farm structures (up to 9,600 m⁻²) and in the intertidal (up to 4,900 m⁻²), although their distribution is very patchy (Kirk et al. 2007).

Baynes Sound, on the east coast of Vancouver Island (49.5°N, 124.8°W), contrasts dramatically with Malaspina Inlet as a foraging landscape for surf scoters. Baynes Sound is a wide, protected channel with low-grade deltas and broad soft-bottom tidal flats. This area has the most intensive shellfish aquaculture in the province, consisting primarily of intertidal culture of clams. Surf scoter prey is almost exclusively clams (Lewis et al. 2007), particularly the commercially cultivated manila clam (*Venerupis philippinarum*) and varnish clams (*Nuttallia obscurata*), an exotic species that was introduced to the region in the early 1990s. The average density of clams in size classes preferred by scoters (20–50 mm) in Baynes Sound is approximately 150 m⁻² (Lewis et al. 2007).

For data collection purposes, each study area was divided into blocks for surveys and functional sites for telemetry. Survey blocks were based on geological habitat features (e.g., headlands, beaches, or rocky shoreline areas) or use designations (e.g., aquaculture lease or marine protected area) with an average shoreline length of 2.3 km (± 0.2 SE) in Malaspina Inlet and 1.8 km (± 0.2 SE) in Baynes Sound. These blocks were subdivided into functional foraging sites used for telemetry locations, which were delineated based on fine-scale habitat features such as bays or reefs and by telemetry range limitations. The foraging sites were roughly of equal size in both study areas and thus facilitated comparisons; mean foraging site size was 1.7 km² in Baynes Sound and 1.5 km² in Malaspina Inlet.

Radio telemetry

Surf scoters were captured in late fall at foraging sites in 2001–2004 using a modified floating mist-net system (Kaiser et al. 1995) and decoys. Birds were banded and weighed, sex was determined by plumage characteristics (Iverson et al. 2003), and age class was estimated by probing bursal depth (Mather and Esler 1999). Either subcutaneous

or internal coelomic VHF transmitters with external antennae were implanted following procedures described by Mulcahy and Esler (1999). Implanted transmitters have been shown to perform well for scoters, with low mortality effects and good signal strength and accuracy (Iverson et al. 2006). In Baynes Sound, 106 surf scoters were radio-tagged over 3 years (2001 $n = 42$; 2002 $n = 37$, 2003 $n = 27$). In Malaspina Inlet, 74 surf scoters were radio-marked in 2004.

Radio-marked scoters were tracked from release until mid-March to document their locations over the winter period. Each individual was located weekly or twice weekly when possible. Fixes were obtained using a null/peak combiner system (Kuechle 2005). In Baynes Sound, fixes were made using two vehicles mounted with four-element Yagi antennae and programmable scanning receivers (Advanced Telemetry Systems, Isanti, MN). Bearings were taken by the two observers simultaneously to obtain bi-angulated locations and processed using the Location of a Signal (LOAS) software (Ver. 2.13, Ecological Software Solutions, Sacramento, CA). Output from LOAS was projected in ArcView 3.2 (ESRI, Redlands, CA) to visually check for accuracy and location data was filtered to remove non-intersecting bearings, upland locations, locations >4 km from observers that may have been unreliable due to weakened signal strength. Error testing of the Baynes Sound system indicated a standard deviation of $\pm 4.2^\circ$ from the true bearing and a mean 90% error polygon of 0.07 km^2 (± 0.004 SE). In Malaspina Inlet, where there was no road access, radio-telemetry was conducted from a boat using a four-element Yagi antenna. An observer obtained two bearings per bird, each from a different location, to allow for bi-angulated locations. Error testing in Malaspina Inlet indicated the standard deviation of bearings was $\pm 6.8^\circ$ and the mean 90% error polygon was 0.02 km^2 (± 0.008 SE; White and Garrott 1990).

Distribution surveys

Surveys were conducted in both study areas to evaluate variation in surf scoter numbers and distributions. In Malaspina Inlet, the surveys followed a fixed route, proceeding at <10 km/h at a distance of 100 m from shore and covered all 34 survey blocks. Surf scoters ≤ 250 m of shore were counted, thus including all foraging habitats. Surveys were conducted monthly from October until April in 2002/2003 and 2003/2004 and weekly in 2004/2005. In Baynes Sound, the study area was divided into 35 survey blocks, each extending 800 m from shore. Counts were made from shore using a spotting scope from one to three observation points per block. The surveys were conducted biweekly from October until April during winters 2002/2003 and 2003/2004 and monthly during winter 2004/2005.

Movement metric analysis

Home range and movement estimates were calculated in ArcView using the Animal Movement extension (Hooge and Eichenlaub 1997). Home ranges were calculated using fixed kernel estimates (Kernohan et al. 2001), with only foraging locations included because our primary interest was ‘foraging range’ rather than total area used. Because accuracy of home range estimates is sensitive to the number of locations (Seaman et al. 1999), we conducted a bootstrap analysis of our data to determine at what sample size foraging range estimates reached a plateau. We determined that foraging range size continued to increase with additional locations beyond the sample size for the majority of our subjects, therefore, we elected to use ten randomly selected locations per individual for kernel estimates using the ‘randomly select points’ function in AME. By standardizing in this way we avoided any bias associated with having different numbers of locations for each individual (Harris et al. 1990). We also calculated the mean distance between consecutive foraging locations (hereafter called interfix distance) using the ‘Location Statistics’ function of AME.

Least square general linear models were used to evaluate variation in foraging range estimates and interfix distances in relation to study area and sex and age classes of individuals. We used an information theoretic approach to model selection (Burnham and Anderson 2002) and calculated Akaike’s Information Criterion (AIC_c) for each model within each candidate set. The candidate set in our analyses consisted of the following models: (1) study area, (2) class, (3) study area + class, and (4) a null or equal means model. The ‘class’ variable always included an individual’s age and sex (for example adult female) owing to sample size restrictions. The same predictors and candidate set of models were used to evaluate both winter foraging range size and interfix distance as response variables. We compared the AIC_c score for each model to that of the best-fitting model (ΔAIC_c) and calculated Akaike weights (w_i) as a measure of the relative support for each model.

Site fidelity analysis

As another measure of movement patterns, we calculated rates of within-winter fidelity to functional foraging sites and compared these between Baynes Sound and Malaspina Inlet. Functional foraging sites were digitized in ArcView into a site shapefile layer and telemetry locations were projected for each radio-marked scoter using the spatial join geo-processing feature in ArcView. We used the known fates modeling procedure in Program Mark (Ver. 4.3, G. C. White, Fort Collins, CO) to assess variation in site faithfulness of surf scoters across study area, sex, and age classes. In our analysis, we replaced the probability that an animal

would die in the interval between detections t and $t + 1$ with the probability it would leave the foraging site where it began the winter period (Bennetts et al. 2001, Iverson and Esler 2006). An encounter history was created for each bird based on 1-week intervals beginning in early December and ending in early March. During each interval, individuals were listed as faithful (stayed within its original foraging site, or a directly adjacent site, during that interval), moved (located in a new site during the interval), temporarily censored (undetected in that interval, but later located), or permanently censored (dead, failed radio, or had moved in a previous interval). Our dataset included 128 individuals with valid encounter histories (Baynes Sound $n = 59$; Malaspina Inlet $n = 69$) and employed a logit link to bound parameter estimates and ensure numeric optimization (Cooch and White 2006). A total of ten models were included in our candidate set, with study area, sex, age, a fully parameterized model of study area + sex + age, and a null model each incorporated with and without time dependency (week). By considering only single variable models of our three primary parameters of interest (study area, sex, and age), we reduced the possibility of Type I errors associated with inferences made from poorly sampled variables (particularly the hatch-year age class in Baynes Sound).

Distributional consistency

Finally, we inferred movements of surf scoters based on the consistency of their distributions over time in each of the two foraging landscapes using data from surveys of the unmarked scoter population. We used a method that generates a distributional consistency (DC) score for surveyed populations in designated areas (Heath 2001). Specifically, DC compares observed distributions of individuals across survey areas (in this case survey blocks) to all theoretically possible distributions, while taking into account the observed changes in overall population size. DC scores are scaled from 0 to 1. A perfectly consistent distribution pattern, where the number of individuals in each block is uniform (given population size changes) across all surveys would score as 1, and would indicate very low levels of movement. A very inconsistent pattern, with disparate bird abundances in blocks across surveys, would have a DC score approaching zero and would indicate high rates of movements among blocks.

For every survey winter (3 years: 2002/2003, 2003/2004, and 2004/2005), we randomly selected one survey per month (November to February) to use in analyses. This gave us a total of four representative surveys per study area per year and eliminated the problem of unequal numbers of surveys in different years across the two areas. A matrix table of total surf scoter numbers across polygons was constructed and applied to the MATLAB (Mathworks Version

7.2) routine as per Heath (2001), to yield a DC score for each year in each area. A mean DC score (\pm SE) was then calculated to compare study areas.

Results

Movement metrics

Marked differences were evident in the local movement patterns of surf scoters in the two study areas. As predicted, birds in Baynes Sound ($n = 35$) had much smaller winter foraging ranges and shorter movement distances than birds in Malaspina Inlet ($n = 34$), which exhibited larger foraging ranges and longer distance movements between consecutive observations (Table 1; Fig. 2). The mean foraging range size of surf scoters from Malaspina Inlet was nearly three times as large as those in Baynes Sound, while interfix distances were more than twice as large (Table 1). In our general linear model analyses of foraging range size and interfix distance, the models, which included study area as the sole variable of interest had the lowest AIC_c score (Table 2). Akaike weights, which were estimated as $w_i = 0.98$ and 0.99 in the two analyses, respectively, indicated that alternate models that included class (sex and age) as a potential explanatory variable did not improve model fit. In fact, in both the foraging range size and infix distance analyses models that included class as the sole explanatory variable ranked below the null model, indicating sex and age were not significant predictors of either movement metric. Overall, variation in range size and movement distances across the age and sex classes was slight as compared to the differences between study areas (Fig. 2).

Site fidelity

Study area was also the variable that best explained variation in site fidelity rates of wintering surf scoters (Table 3). In

Table 1 Summary of results for movement metrics of surf scoters wintering in Baynes Sound ($n = 35$) and Malaspina Inlet ($n = 33$), British Columbia

Movement metric		Baynes Sound (clam habitat)	Malaspina Inlet (mussel habitat)
Winter foraging range (km ²)	Mean	2.7 \pm 0.8	10.3 \pm 1.2
	Median	1.0	8.0
	Range	0.1–20.8	0.4–26.8
Average distance between successive locations (km)	Mean	0.6 \pm 0.1	1.9 \pm 0.2
	Median	0.5	1.7
	Range	0.1–2.6	0.5–4.0

Means are reported \pm SE

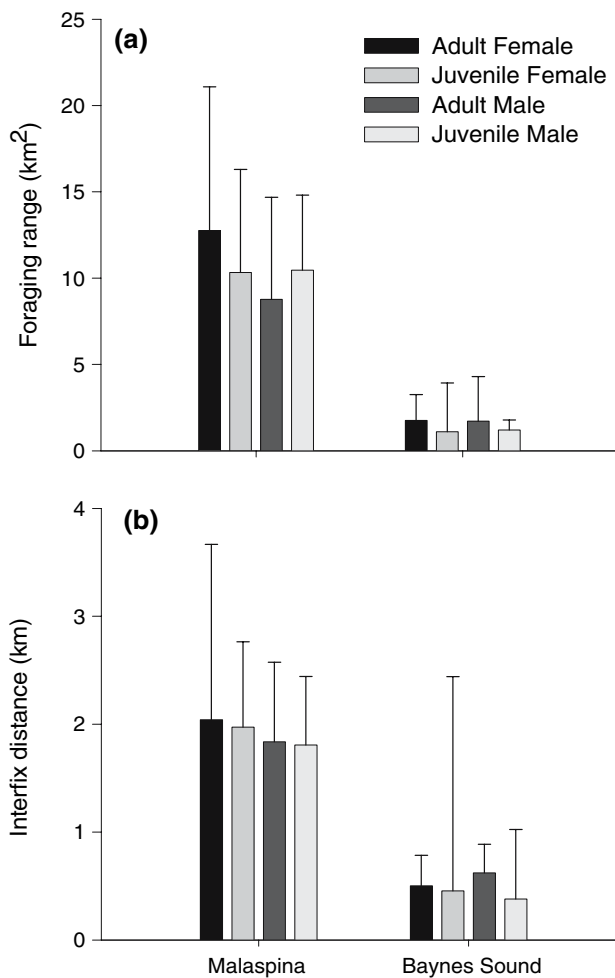


Fig. 2 **a** Winter foraging range size (km^2) and **b** interfix distance (km) for all cohorts of surf scoters from Malaspina Inlet ($n = 33$ individuals; 5 adult females, 9 juvenile females, 7 adult males and 12 juvenile males) and Baynes Sound ($n = 35$ individuals; 8 adult females, 2 juvenile females, 22 adult males and 2 juvenile males), mean + 95%CI

Table 2 Summary of AIC results from general linear models assessing variation in winter foraging range size (km^2) and mean interfix distance (km) for surf scoters from two distinct habitats (Baynes Sound and Malaspina Inlet) in the Strait of Georgia, BC

Response variable	Model	Number of parameters	ΔAIC_c	AIC_c weight	R^2
Foraging range	Study area	4	0.00	0.98	0.31
	Study area + class	8	8.41	0.02	0.32
	Null	2	20.85	0.00	0.00
	Class	6	24.59	0.00	0.07
Mean interfix distance	Study area	4	0.00	0.99	0.43
	Study area + class	8	9.54	0.01	0.43
	Null	2	34.20	0.00	0.00
	Class	6	36.62	0.00	0.09

Models with the 'class' parameter include sex (male or female) and age (adult or hatch-year) additively. Number of parameters includes +1 for intercept and +1 for model variance. Candidate sets are listed by ΔAIC_c

Table 3 Summary of AIC model selection results for modified Kaplan–Meier site fidelity analysis

Response variable	Model	Number of parameters	ΔAIC_c	AIC_c weight
Site fidelity	Study area	2	0.00	1.00
	Study area + week	24	16.42	0.00
	Week	12	82.73	0.00
	Age	2	83.89	0.00
	Sex + week	24	87.52	0.00
	Null	1	90.40	0.00
	Sex	2	91.65	0.00
	Age + week	24	94.36	0.00
	Study area + sex + age + week	96	143.33	0.00

Models including week as a parameter allow site fidelity to differ in each of the 12 week intervals. Otherwise, models were time independent. Candidate set is listed in order of ΔAIC_c

our known fates analysis the model that included study area and no time dependency had an Akaike weight of $w_i = 1.00$. Study area + week was the next best fitting model, but had a $\Delta\text{AIC}_c = 16.42$, indicating that adding time dependence did little to improve model fit. Models including sex and age class had $\Delta\text{AIC}_c > 80$, suggesting these variables had little to no predictive power for estimating the probability of site fidelity. Consistent with our movement metric results, surf scoters in Baynes Sound exhibited higher site fidelity (cumulative fidelity = 0.83) than Malaspina Inlet (cumulative fidelity = 0.04) (Fig. 3). This indicates that a comparatively large proportion of scoters from Baynes Sound remained faithful to one foraging site all season long, while the majority of surf scoters in Malaspina Inlet moved to occupy two or more foraging sites over the course of the winter.

Distributional consistency

DC scores indicated more consistent monthly distributions in Baynes Sound (Table 4). Malaspina Inlet DC scores were lower than Baynes Sound in every year and when years were combined. Therefore, throughout the season there were more changes in the distribution of scoters across survey blocks in Malaspina Inlet than in Baynes Sound. The lower within-season DC scores in Malaspina Inlet (Table 4) suggest surf scoters there displayed a higher level of movement.

Discussion

Previously, few studies had the opportunity to examine the movement behaviors of a predator species as a facultative

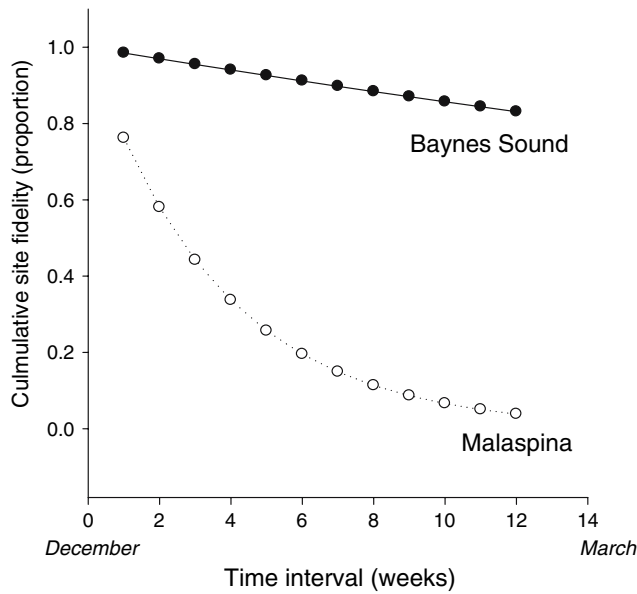


Fig. 3 Site fidelity functions of surf scoters in Baynes Sound ($n = 59$, filled circle) and Malaspina Inlet ($n = 69$, open circle), based on model averaged parameter estimates in the Kaplan–Meier analysis. Cumulative fidelity can be interpreted as the proportion of marked birds in each study area that remained in their original foraging site through winter

Table 4 Distributional consistency scores over 3 years of surf scoter surveys at each study area, as well as a 3 year mean \pm SE

Year	Baynes Sound	Malaspina Inlet
2002/2003	0.72	0.16
2003/2004	0.63	0.24
2004/2005	0.50	0.35
Within-season mean DC \pm SE	0.62 \pm 0.06	0.25 \pm 0.05

response to variation in prey. By combining radio telemetry and distribution data, we quantified the space use of surf scoters in a system where predators naturally occurred in two areas with strongly differing prey landscapes. This allowed for a unique empirical field study of the influence of habitat and prey type on movement patterns. We found strong agreement with foraging and distribution theory. The space use and movements by surf scoters in the Strait of Georgia were strongly related to the winter habitat they occupied. Surf scoters displayed high site fidelity, small foraging range size, limited movements, and very consistent distribution patterns while wintering in the soft-bottom clam habitats of Baynes Sound. In contrast, in the rocky mussel habitats of Malaspina Inlet, surf scoters exhibited large foraging ranges and long distance movements, little seasonal faithfulness to foraging sites and much less predictable distribution patterns throughout the winter. Despite empirical evidence and theoretical suggestions of increased

movement and dispersal by juveniles and males (Robertson and Cooke 1999; Cooke et al. 2000), we found that sex and age class were not important determinants of any movement metric. We infer that observed differences in movements were related to habitat differences, and conclude that this is evidence of environmentally mediated predator behavior.

Expectations derived from the IFD and optimal foraging theories predict how the spatial distribution and temporal stability of resources influence movement patterns of predators. We suggest that differences in the foraging landscapes between our study areas led to the observed differences in movement patterns. Larger home ranges and higher movement probabilities, like those observed in Malaspina Inlet, are often associated with lower quality resources, higher rates of prey depletion, or an increased degree of prey variability (Tufto et al. 1996; Marzluff et al. 1997; Ferguson et al. 1999). In this case, mussels were more susceptible to depletion, a prey attribute that has important ecological implications for foraging predators (Charnov et al. 1976). Meanwhile, the high foraging site fidelity and small ranges of scoters in Baynes Sound are indicative of a stable prey resource with high over-season availability and low levels of variability (Warnock and Takekawa 1996; Fisher 2000; Smith and Schaefer 2002). These findings are consistent with foraging theory and indicate that predators modify their behavior in response to the foraging landscape.

It is well documented that wintering sea ducks can deplete food stocks (Guillemette et al. 1996). Large flocks of communally foraging scoters attracted to high density, clumped mussels can cause total extirpation of local resources (Lacroix 2001). In Malaspina Inlet, mussels were severely depleted within the study area (95% decline; Kirk et al. 2007). This dramatic change in the food supply in Malaspina Inlet implies that surf scoters there may have been exposed to prey densities below their critical movement threshold. This induced surf scoter movements to new foraging sites, within and outside the study area, thereby increasing range sizes, reducing site fidelity estimates, and leading to changes in distribution patterns (resulting in low DC scores). Emigration and dispersal by predators also can often be attributed to the reduction of food availability or higher variability of resources (Lurz et al. 1997). In all years of the study, the total number of surf scoters in Malaspina Inlet began to decline in early January as birds departed, presumably in search of more profitable foraging patches outside the survey area (Kirk 2007). By contrast, low rates of prey depletion in Baynes Sound likely did not lead to depression of resources below the movement threshold for surf scoters wintering there. Baynes Sound birds exhibited high fidelity, small foraging ranges, and a very consistent distribution across sites throughout the year. The

total number of surf scoters was also more constant than in mussel foraging sites. A recent study in Baynes Sound showed that scoters there are not constrained by amount of daylight (i.e., they do not forage nocturnally, Lewis et al. 2005) nor by prey availability, as foraging effort did not increase as clams were depleted (Lewis et al. 2008). Together, these data corroborate the conclusion that Baynes Sound is a highly stable winter habitat for scoters.

The significant depletion of mussels in Malaspina Inlet indicates that this area is a high quality habitat that is heavily used by ducks. When prey densities are sufficiently high, i.e., early in winter, mussel habitats may be very profitable, due to the reduction or elimination of dive, search and handling times. The mussels available on Malaspina Inlet shellfish aquaculture structures were not only abundant and visible, but occurred on floating or very shallow structures, reducing foraging costs relative to dives required to search for clams (De Leeuw 1996). The energetic costs of diving may be an especially important constraint for ducks in winter, already facing high thermoregulation costs and daylight limitations. Mussels are generally swallowed underwater and require no surface handling time (De Leeuw 1999), while larger prey such as clams have a capture success rate of only 50% (Lewis et al. 2008) and may require significant surface handling time, thus increasing time investment in each prey capture (Guillemette et al. 1992). Foraging on mussels also allows scoters to minimize shell intake. The shell minimization theory suggests that molluscivores may select for a less energy-rich prey item to reduce the amount of shell they must process (Bustnes and Erikstad 1990; Hamilton et al. 1999). The shell mass of mussels is much less than the thicker-shelled clam species that dominant the diet of Baynes Sound scoters (D. Esler, unpublished data). Finally, surf scoters are especially adept at using ephemeral resources on an opportunistic basis (Lacroix et al. 2005). Our data indicate that high numbers of scoters pass through the Malaspina Inlet area in early winter (Kirk 2007), to profit from the high abundance of accessible mussels that recruit on aquaculture structures, and many move on to more stable wintering areas, like Baynes Sound.

Over-winter survival estimates are similar for surf scoters from Baynes Sound and Malaspina Inlet (D. Esler, unpublished data), and we assume that the overall energetic costs and benefits of the two prey landscapes must balance out. While mussel foragers invest more time and energy in moving from site to site, their costs of diving and searching for prey are reduced. Surf scoters in clam habitats benefit from maintaining small winter foraging ranges, but must cope with greater investment in searching and handling required for foraging on the more cryptic clams. This study used multiple data types and a species that naturally occurs

in different habitats to examine a predator's facultative responses to variation in habitat and prey. Our findings were consistent with foraging theory: habitat and prey type of the foraging landscape have a strong influence on the movement strategies of surf scoters. By understanding the ecological basis for these movement patterns, we have gained important insight into the winter habitat requirements of scoters that will assist in the conservation and management of their populations in British Columbia's changing coastal environment.

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