HABITAT USE AND BEHAVIOR OF THE PACIFIC SAND LANCE (*AMMODYTES HEXAPTERUS*) IN THE SHALLOW SUBTIDAL REGION OF SOUTHWESTERN VANCOUVER ISLAND

TREVOR B HAYNES, ROBERT A RONCONI, AND ALAN E BURGER

Department of Biology, University of Victoria, Victoria, British Columbia, V8W 3N5 Canada

ABSTRACT—The Pacific Sand Lance (*Ammodytes hexapterus*) is an important Pacific Northwest prey species for marine predators. In our study along the West Coast Trail, southwestern Vancouver Island, British Columbia, we examined shallow subtidal habitat selection of juvenile and adult Sand Lance with respect to sediment characteristics, and also examined aggregation behavior. Analysis of presence or absence using a classification tree showed that Sand Lance avoided sites with no subtidal sediments, preferred sites with mean sediment particle sizes ≤1290 μm and preferred mixed sediments (sorting values >3.09 standard deviations; standard deviation of particle size used as a heterogeneity index of the substrate grain size). The regression tree analysis explained 99% of the variation in abundance based on the effects of mean particle size, particle sorting and presence or absence of sediments, but the model showed evidence of over-classification due to small sample sizes. Nevertheless, the model indicated environmental factors that are important for Sand Lance habitat use. Behavioral analysis showed that Sand Lance aggregated into larger schools to feed and these schools tended to occur in the mid-water column compared to non-feeding schools which remained closer to the seafloor. Near the beaches, 0-year (young-of-the-year) Sand Lance were found in deeper water compared to older Sand Lance (1^+-year classes). Together these data suggest that Sand Lance using the shallow subtidal show some indication of habitat use based on particle size and sorting, and aggregation differences based on behavior and age class.

Key words: Pacific Sand Lance, *Ammodytes hexapterus,* habitat selection, schooling behavior, classification tree, southwest Vancouver Island

Fishes of the genus *Ammodytes* are preyed upon by seabirds, marine mammals, and piscivorous fishes throughout their ranges and are considered critical links between zooplankton and top marine predators (Springer and Speckman 1997; Willson and others 1999). *Ammodytes* spp. are highly efficient in the transfer of energy from secondary producers to top predators (Anthony and others 2000), can occur in high abundances (for example Abookire and Piatt 2005), and reach their maximum energetic value during feeding periods important for top predators (Robards and others 1999). Variations in availability and distribution of *Ammodytes* spp. have been shown to affect predator populations, with the majority of the research focused on the reproductive success of seabirds (for example Monaghan 1992; Lewis and others 2001; Suryan and others 2002; Litzow and others 2002; Litzow and Piatt 2003; Hedd and others 2006). Low availability of *Ammodytes* spp. is thought to be responsible for large scale breeding failure of numerous seabird species (Vermeer 1979; Martin 1989; Uttley and others 1989; Avery and others 1992; Hamer and others 1993; Hayes and Kuletz 1997).

Pacific Sand Lance (*Ammodytes hexapterus,* hereafter ''Sand Lance'') are abundant in nearshore regions of the Pacific Northwest, being found most commonly in water less than 40 m in depth (Ostrand and others 2005). Seasonally, they appear in the nearshore regions during spring and summer months (Field 1988) and likely remain buried in the sediment in a state of dormancy throughout the winter (O'Connel and Fives 1995; Robards and Piatt 1999). During spring and summer months these small eel-like fish are considered epibenthic, schooling pelagically during the day in order to forage and burrowing in benthic substrate at night (Hobson 1986). It is thought that Sand Lance use burrowing habitat as a refuge in order to

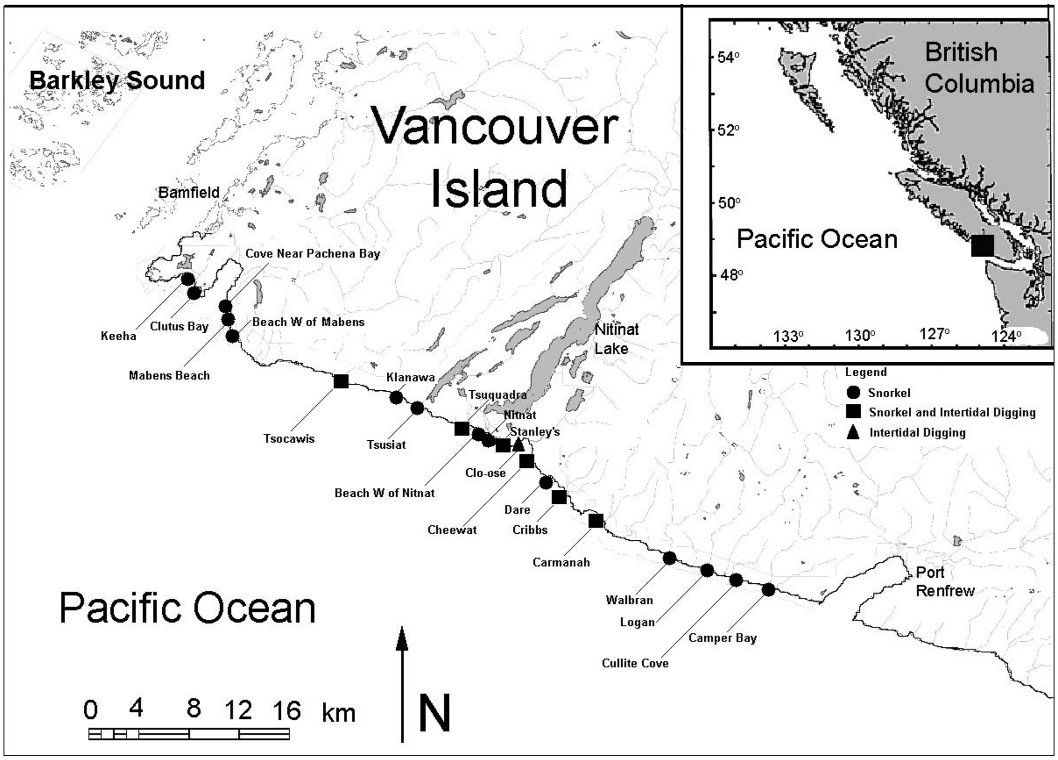


FIGURE 1. Map of the study area and surrounding region showing sites sampled for Pacific Sand Lance (*Ammodytes hexapterus*).

conserve energy and avoid high levels of predation (Dick and Warner 1982; Quinn 1999). The burrowing behavior of Sand Lance causes its habitat use to be strongly tied to highly specific substrates of well-drained coarse sand and small pebbles without mud and silt (Robards and Piatt 1999; Haynes 2006). The use of sediment as a refuge also causes Sand Lance to be associated with shorelines having large deposits of substrate suitable for burying (Ostrand and others 2005; Haynes 2006).

Due to the absence of a commercial fishery for Sand Lance in the northeastern Pacific, there have been few studies of their biology, and factors affecting their abundance and distribution remain poorly known (Field 1988; Robards and Piatt 1999). This is particularly true for British Columbia where there have been few ecological studies of this species (Haynes 2006). In this study we examine the habitat use of juvenile and adult Sand Lance in a shallow subtidal region off southwest Vancouver Island, focusing on sediment properties (an important habitat requirement) and aspects of their behavior.

METHODS

Study Area

The study was conducted between 29 May and 4 August 2006 within the West Coast Trail (hereafter WCT) unit of the Pacific Rim National Park Reserve of Canada on the west coast of Vancouver Island, British Columbia (Fig. 1). We used the park boundary to delineate the study area that consists of approximately 78 km of coastline, with a southwestern exposure to the Pacific Ocean.

Snorkeling Surveys

We sampled Sand Lance subtidally using snorkeling surveys, a technique which has been shown to out-perform other methods in detecting Sand Lance in shallow subtidal areas (Haynes 2006). Site selection was based on the presence of intertidal sediment extending into the subtidal region (thus referred to as beaches). We sampled approximately 90% of major beaches (longer than 50 m) within the study area (Fig. 1). In addition, we surveyed 4 nonbeach sites that included exposed rocky shelves and sandy shorelines with a rocky intertidal and subtidal (Beach W of Mabens, Camper Bay, Cullite Cove, Tsusiat). We sampled 15 of the 20 sites twice and 1 site 3 times.

At each site, 2 observers using masks, snorkels and fins swam along 2 independent transects parallel to the shoreline, 1 each along the approximate 4 m and 8 m bathymetric contour for the length of the beach. Snorkelers continuously dove from the surface to the bottom as they swam in order to observe the entire water column. Snorkel transects ran the entire length of the intertidal sand of the shoreline. Observers recorded the abundance, behavior, fish size, depth and position in the water column of each Sand Lance aggregation. Abundance was estimated by counting a subsample of Sand Lance within a given area and then visually extrapolating to the entire Sand Lance school. We took GPS waypoints at the start and end of each transect in order to measure transect distances. Water visibility was measured using a Secchi disc (40 cm diameter). Surveys were undertaken only when water clarity was good (Secchi depth >3 m) and when sea conditions were favorable (low swell-wave height). For each snorkel site, sediment samples were extracted from the center point of the 8-m transect using a ponar grab or by a snorkeler and used for grain size analysis.

Intertidal Digging

Sand Lance can remain buried in the intertidal sediment even after the tide recedes, using interstitial water for respiration (Quinn 1999). Digging in the intertidal sediment on a low tide is an effective method for sampling buried Sand Lance (Dick and Warner 1982; Robards and others 1999; Haynes 2006). We sampled for Sand Lance in the intertidal by digging just above the low tideline at extreme morning low tides (tide range: 0.43–0.65 m). Due to the tidal restriction on sampling and the logistics involved, we were only able to sample 7 sites, each sampled once.

Every 75 m, we dug a series of 5 pits just above the tide line approximately 8 m apart. The pits were 1 m^2 in area and 8 cm deep. Samples of the intertidal substrate (1–4 from each site, depending on beach length) were extracted for lab analysis using a plastic plug 8 cm deep (mean dried mass = 441, s = 129 g).

Sediment Characteristics

Subtidal regions were categorized by presence-absence of sediment (Sediment Presence-Absence) and incorporated in models as a binary variable (1/0 respectively). Sites with 100% bedrock were considered to have sediment absent. Intertidal and subtidal samples were processed using dry sieving techniques (Folk 1974). First, sediment was dried in an oven for 24 h at 100°C (intertidal and subtidal mean dried mass was $\bar{x}$ = 441, s = 129 g and $\bar{x}$ = 351, s = 154 g, respectively). The samples were added to the top of a stack of 12 metal sieves ranging from 24,500 to 44 μm. A mechanical shaker agitated the sieves for 15 min. After agitation, each particle size class was weighed to the nearest 0.001 g. Weights were entered into the GRADISTAT statistical package (Blott and Pye 2001) to analyze the particle size distribution statistics. We chose the Folk and Ward (1957) graphical technique, recommended by Blott and Pye (2001), for determining Particle Size Mean (μm) and Particle Sorting (standard deviation of the mean). These two measures are important physical descriptors of sediment and have been linked to Sand Lance use of sediment as burying habitat (Haynes 2006). Particle Size Mean limits Sand Lance burying behavior physically as Sand Lance are only able to bury in a specific range of particle sizes (Pinto and others 1984). Particle Sorting, the standard deviation of Particle Size Mean, is another important physical factor in determining whether the sediment is suitable for burying. As sediment transported by water settles, it is deposited according to grain size. This creates a distribution of grain sizes. Thus, sorting describes the heterogeneity of the substrate grain size, whether the substrate is a mix of different sized grains or whether it is relatively homogeneous.

Sediment characteristics of intertidal substrate samples were compared to the sediment characteristics of sites where Sand Lance were found in the intertidal by Haynes (2006) in Barkley Sound, approximately 15 km north of the WCT. The comparison was made using a Mann-Whitney U test. No shallow subtidal sediment samples were collected in Barkley Sound thus between site comparisons were restricted to intertidal substrates to give context to our results regionally.

Habitat Analysis

We examined Sand Lance habitat use in terms of 2 dependent variables: Sand Lance Presence-Absence and Sand Lance Abundance. Sand Lance Presence-Absence was coded as present (site has >1 Sand Lance present) or absent (site has 0–1 Sand Lance present). Sites with only 1 Sand Lance present were included in the absent category because the sighting of 1 Sand Lance was not considered sufficient evidence that they were using the site. Sand Lance are most regularly found in schools thus the presence of 1 Sand Lance is likely due to a stochastic event rather than active habitat selection. Sand Lance Abundance was calculated by combining the abundances from individual snorkelers for each site and dividing by the total linear distance traveled by both snorkelers. For sites with more than 1 sampling event, abundance was measured as the mean abundance for all sampling events.

All statistical analyses were conducted using SPSS 14.0. Twenty sites were used in all habitat analyses. Using Sand Lance Presence-Absence as the dependent variable, we ran a binary logistic regression analysis using Particle Size Mean, Particle Sorting, the interaction term between the 2, and Sediment Presence-Absence (classification cut-off = 0.5, maximum iterations = 20). We also constructed a classification tree for Sand Lance Presence-Absence with the 3 independent variables in order to provide an alternative view using a different modeling technique. The tree was constructed using the Classification and Regression Tree (CART) algorithm and then pruned using the 1 standard-error rule (Breiman and others 1984). Pruning helps prevent overfitting (growing extremely large trees that overfit the data) and is analogous to variable selection in regression (Moisen and Frescino 2002). Because preliminary screening of data showed that sites with sediment absent had a perfect negative association with Sand Lance Presence-Absence, Sediment Presence-Absence was forced as the 1st variable in the model.

The tree was validated using a V-fold cross-validation (Breiman and others 1984), which is 1 of the preferred ways of pruning back the original tree as it can be used to validate the model, or when the training data set is too small to remove a test sample set. After the growth has been terminated, the V-fold cross-validation prunes the tree by randomly partitioning the data into V groups (in this case 10) of equal or similar size. A classification tree of a specified size is built using 9 of the 10 groups and evaluated with the withheld group. This is done iteratively with each of the 10 groups being withheld and repeated for each of the considered tree sizes, starting with the terminal tree and continuing until the parent node is reached. The resulting 10 cross-validation costs for each tree size can then be averaged giving the final estimate of the 10-fold cross-validation cost for each size. The cross-validation procedure produces a ''risk estimate'' which estimates the classification error. In addition to cross-validation, we used simple re-substitution to evaluate the model where the original data are substituted directly into the model to determine how well the model predicts the data set used to build it.

Using Sand Lance Abundance as the dependent variable, we constructed a regression tree using the same CART method with the same 3 independent variables. Sediment Presence-Absence was not forced as the 1st variable in this model.

Behavioral Analysis

Sand Lance behavior was observed during the snorkeling surveys, and recorded in 5 categories: schooling (aggregated, moving as a group and not feeding), feeding (Sand Lance seen actively feeding on plankton), balling (forming tight stationary aggregations in the shape of a ball), shoaling (loose aggregations not moving as a group and not feeding), and streaming (schooling in a long narrow formation). Feeding Sand Lance were distinguished from other classifications as loose formations observed consuming prey in the water column. We explored relationships between these behavior categories and 5 environmental variables: Size Class, Depth, Water Column, Tide Height and Abundance.

Size Class was a binary classification categorizing the dominant year class of the school: 0-year (young of the year, <90 mm), 1^{+}-year (Sand Lance 1 year and older, >90 mm). Depth was the recorded distance between seafloor and the surface of the water at the point that Sand Lance schools were seen. Water Column was the position of the school in the water column ranging from 0% (surface) to 100% (seafloor). Tide Height represents the tide level when the snorkel survey was conducted (m). Abundance was the number of Sand Lance in the school (ln transformed).

We used Mann-Whitney U tests to determine whether there was a relationship between the continuous variables and the categorical variables. The resultant *P*-values were adjusted using Holm's (1979) correction for multiple comparisons. We performed a chi-square test to determine whether there was a relationship between Size Class and Behavior (the 2 categorical variables). We constructed a nonparametric correlation matrix to look for relationships among the 4 continuous variables. Statistical tests were considered significant at 5% level of significance.

RESULTS

We snorkeled over 38 km along 16 beach and 4 non-beach habitats. Because transects were based on bathymetric contours, distance between transects varied between sites based on the slope of the seafloor ($\bar{x}$ = 126, s = 58 m). During these surveys we documented 202 Sand Lance aggregations (mean aggregation size = 1097, s = 2041 Sand Lance). Sand Lance were noted to form mixed-species schools with juvenile Pacific Herring (*Clupea harengus*) and juvenile rockfish (*Sebastes* spp.); 7 and 3 aggregations respectively. Sand Lance were found on 57% of surveys at average linear densities of 2.5 Sand Lance/m. Of the 16 sites that were sampled more than once, 14 (87.5%) showed consistency with Sand Lance detection based on snorkel surveys, defined as uniformity in presence or absence in sampling repeated through the season (Table 1). In both inconsistent cases, Sand Lance were absent in June but present in late July.

At Stanley's Beach, Sand Lance were found during both sampling events, however, during the 2nd survey they were found outside of the snorkel transects. In the 1st survey at Stanley's Beach, Sand Lance were found within approximately 0.5 m of the bottom in high abundance but spread out in low density shoals, staying close to the bottom possibly to avoid predation or wave energy. During the 2nd sampling event, Sand Lance were not seen during the snorkel surveys despite traveling over the original transect lines. However, Sand Lance were seen by snorkelers in kelp beds (Bull Kelp, *Nereocystis leutkeana*) further offshore in areas dominated by bedrock, actively feeding in large dense schools in the upper half of the water column in an area not included in the original snorkel transects.

Intertidal Digging

No Sand Lance were found in the intertidal digging surveys on the WCT (150 pits dug at 30 points on 7 beaches). A total of 18 sediment samples were taken from 7 beaches. No significant differences were seen in the intertidal sediment characteristics found in the WCT compared to those found in Barkley Sound (Haynes 2006) using the Mann-Whitney U test (Particle Size Mean, U = 106.0, n_1 = 16, n_2 = 18, P = 0.190; Particle Sorting, U = 96.0, n_1 = 16, n_2 = 18, P = 0.098). Haynes (2006) reported Sand Lance at 27% of 55 beaches with these characteristics in Barkley Sound. The absence of Sand Lance on WCT beaches was therefore not due to major differences in sediment characteristics. The region is exposed to the Pacific Ocean and receives higher wave action than Barkley Sound. The mean wave height (Neah Bay Ocean Buoy 46087, 48.49° N 124.73° W) between May and July was 1.4 ± 0.6 m (National Buoy Data Center, accessed 10 July, 2007).

Sand Lance Presence-Absence

Sand Lance were present at 12 (60%) of the 20 study sites. We never found Sand Lance at the 4 sites without sediment (Table 1), and these sites were excluded from analysis of grain size effects. A logistic regression analysis to test for sediment effects was run with the 16 remaining sites (12 with Sand Lance present, 4 with Sand Lance absent). This analysis revealed that Sand Lance presence or absence could be predicted by Particle Size Mean, Particle Sorting and the interaction term Particle Size Mean × Particle Sorting (Table 2). The logistic regression model had completely homogenous classification with a pseudo R-squared value of 0.675, (2LL $<$ 0.001, model χ^2 = 17.995, df = 3, $P < 0.001$; Hosmer and Lemeshow goodness-of-fit test $<$ 0.001, df = 2, P = 1.00). Further examination of independent variables

TABLE 1. Sand Lance detection consistency for all sites. Consistency refers to the uniformity in detection of Sand Lance at a site. Numbers in columns represent Sand Lance Abundance values (Sand Lance m^{-1}). ''na'' indicates where Changes in Abundance and Consistency were not applicable because the sites were only sampled once.

Site	Late May	Late June	Early July	Late July	Early August	Change in Abundance	Consistency	Subtidal sediment P/A
Mabens Beach		1.708			0.592	decrease	Y	P
Cullite Cove		0		0		decrease	Y	A
Walbran			8.457	0.260		decrease	Y	P
Cheewat			0.073	0.359		increase	Y	P
Cove near Pachena Bay		0.238			6.471	increase	Y	P
Cribbs				0.866	2.950	increase	Y	P
Keeha Bay		0**		7.439		increase	N	P
Logan		66.667	79.137			increase	Y	P
Stanley's		17.467		40.393*		increase	Y	P
Tsuquadra	0			7.786		increase	N	P
Carmanah			8.334	14.958	7.856	increase, decrease	Y	P
Beach west of Mabens		0			0	same	Y	A
Beach west of Nitinat		0		0		same	Y	P
Camper Bay		0		0		same	Y	A
Nitinat Narrows		0		0		same	Y	P
Tsocawis				0	0	same	Y	P
Clutus Bay				0		na	na	P
Dare				0.898		na	na	P
Klanawa				0.002		na	na	P
Tsusiat			0			na	na	A

* Sand Lance seen by snorkelers post-survey after being detected from the boat.
** Sand Lance seen from the boat but not in snorkel survey.

TABLE 2. Results from the logistic regression run to predict presence or absense of Sand Lance at 16 sites with sediment present on the West Coast Trail.

Variable	Coefficient	S.E.	Wald
Constant	682.6	14.9	<0.001
Particle size mean	−0.4	42.3	<0.001
Particle sorting	−246.8	23968.5	<0.001
Particle size mean × particle sorting	692.7	65835.7	<0.001
Model statistics			
Model chi-square [df]		17.995 [3]	
Sensitivity (% correct predictions)		100	
Specificity (% correct predictions)		100	
Overall (% correct predictions)		100	
Cox and Snell pseudo R^2		0.675	
Area under the ROC curve		0.964	

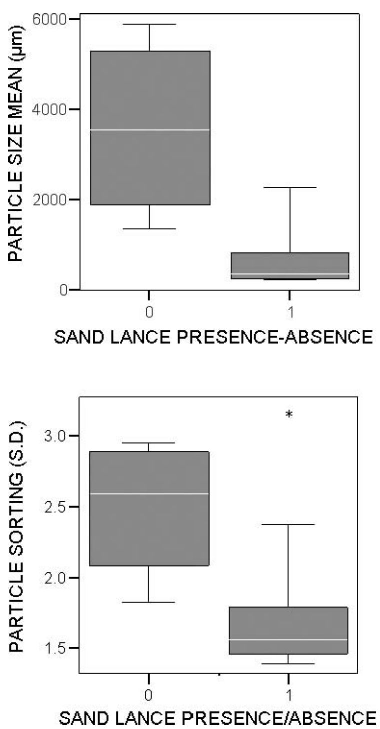


FIGURE 2. Boxplots of the 2 quantitative sediment variables versus Pacific Sand Lance Presence-Absence (1/0 respectively). The upper and lower quartiles are represented by the boxes, the median by the white line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values. * Extreme outlier (>3 times the interquartile range from the median).

showed that sites with Sand Lance present had a lower Particle Size Mean and Particle Sorting than sites with Sand Lance absent (Fig. 2).

The classification tree had similar results showing perfect re-substitution classification (pure terminal nodes, Fig. 3) with Particle Size Mean, Sediment Presence-Absence, and Particle Sorting having importance values of 100%, 89.7% and 75.0%, respectively. The Sediment Presence-Absence variable split the parent node (Node 0) with all sites with sediment absent also having Sand Lance absent (Node 2). This suggests that Sand Lance avoid sites with sediment absent. Node 1 was further split with the Particle Size Mean value of 1290 µm, with all sites with values equal or less having Sand Lance present (Node 3). This suggests that Sand Lance avoid large sediment size and use sites with finer sediments. Node 4 was further split with a Particle Sorting value of 3.07 standard deviations, with 4 of the 5 sites of the node having values less than this cut off (Node 5) and all 4 being sites where Sand Lance were absent. The remaining site had a value greater than 3.07 and Sand Lance were present (Node 6). Cross-validation produced a risk estimate of 0.15 (S_x = 0.08) indicating that the model would have a 15% classification error.

Sand Lance Abundance

Sand Lance Abundance was highly skewed even after transformation, such that most sites had <0.5 Sand Lance m^{-1}. We applied a regression tree model, which is insensitive to violations of normality, to explain Sand Lance abundance relative to sediment characteristics. The resulting tree had 2 splits with 3 terminal

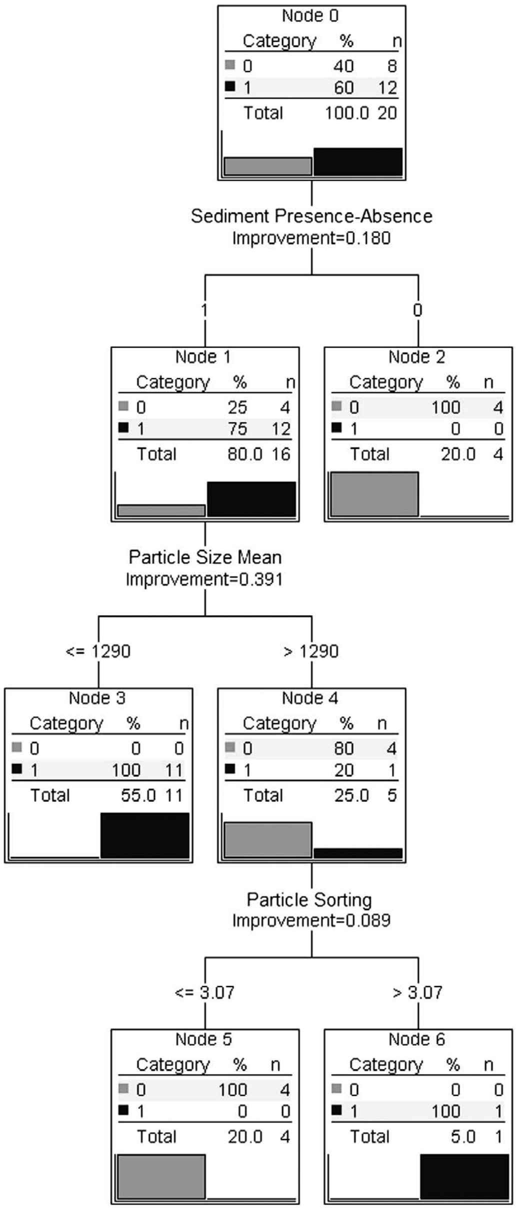


FIGURE 3. Classification tree for Pacific Sand Lance (*Ammodytes hexapterus*) Presence-Absence (0 = Absent, 1 = Present). Splits are created using the variable with the highest predictive power, maximizing the homogeneity of the 2 resultant nodes. ''Improvement'' refers to the decrease in node impurity resulting from the split. Histograms represent the relative frequency of Sand Lance absent sites (grey) to Sand Lance present sites (black) within the node.

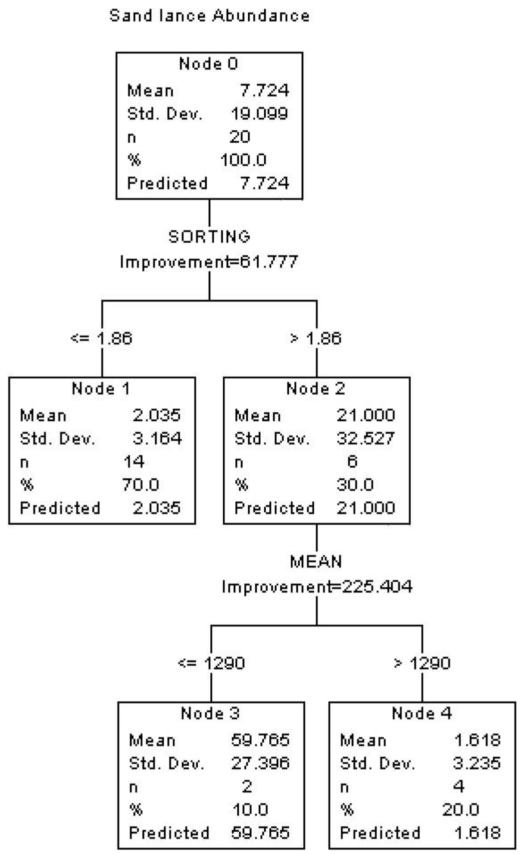


FIGURE 4. Regression tree for Pacific Sand Lance (*Ammodytes hexapterus*) Abundance constructed using 3 independent variables (Particle Size Mean, Particle Sorting and Sediment Presence-Absence). ''SORTING'' represents Particle Sorting (standard deviations) and ''MEAN'' represents Particle Size Mean (μm). ''Improvement'' refers to the decrease within-node variance (computed as the least-squared deviation).

nodes, used 2 of the 3 independent variables in the analysis, and explained 99.4% of the variation in abundance (Fig. 4). Particle Size Mean, Particle Sorting, and Sediment Presence-Absence were given importance values of 100%, 31.4% and 9.5%, respectively. Sediment Presence-Absence was not used in the final model.

Analysis of Behavior and Size Class

Only 2 behavioral categories (Feeding and Schooling) provided sufficient data to test for factors affecting them. Significant differences were found between these categories for Abundance, Tide Height, and Water Column, but not

TABLE 3. Results from the Mann-Whitney U tests for the four continuous variables (rows) grouped by each categorical variable (columns). Size Class and Tide Height were not compared due to a lack of a theoretical basis for comparison. ''YOY'' represents young of the year size class (0-year) while ''1+'' represents the 1+-year size class (all other year classes).

	Behavior				Size class			
Variable	Value	Mean rank [N]	Mann-Whitney U	P-value	Value	Mean rank [N]	Mann-Whitney U	P-value
Abundance	Feeding	67.4 [13]	125.5	<0.001*	YOY	55.9 [78]	908.5	0.188
	Schooling	37.3 [70]			1+	47.0 [28]		
Tide Height	Feeding	28.1 [14]	288.5	0.027				
	Schooling	43.1 [66]						
Depth	Feeding	38.8 [14]	438	0.526	YOY	58.9 [77]	626.5	0.001*
	Schooling	43.2 [70]			1+	36.9 [28]		
Water Column	Feeding	23.0 [11]	187	0.010*	YOY	42.8 [67]	588	0.022
	Schooling	40.0 [63]			1+	56.5 [25]		

Depth (Table 3). Relative to non-feeding schools, feeding schools had significantly higher abundance and were found significantly higher in the water column (Table 3, Fig. 5A, B). Feeding schools tended to form at lower tide height but this difference was not significant when the Holm's correction for multiple comparisons was applied.

The 2 size classes (0-year and 1^+-year classes) showed a significant difference in water depth: 0-year class individuals were found in deeper water (Table 3, Fig. 5C). The size classes showed no significant differences in abundance or position in the water column once the Holm's correction was applied (Table 3). No significant difference was found between the size class of Sand Lance that was feeding versus the size class that was schooling (χ^2 = 0.015, df = 1, P = 0.902). Spearman's rank nonparametric correlation tests showed no significant relationships between Sand Lance abundance and any continuous independent variable (Depth, Tide Height, and Water Column).

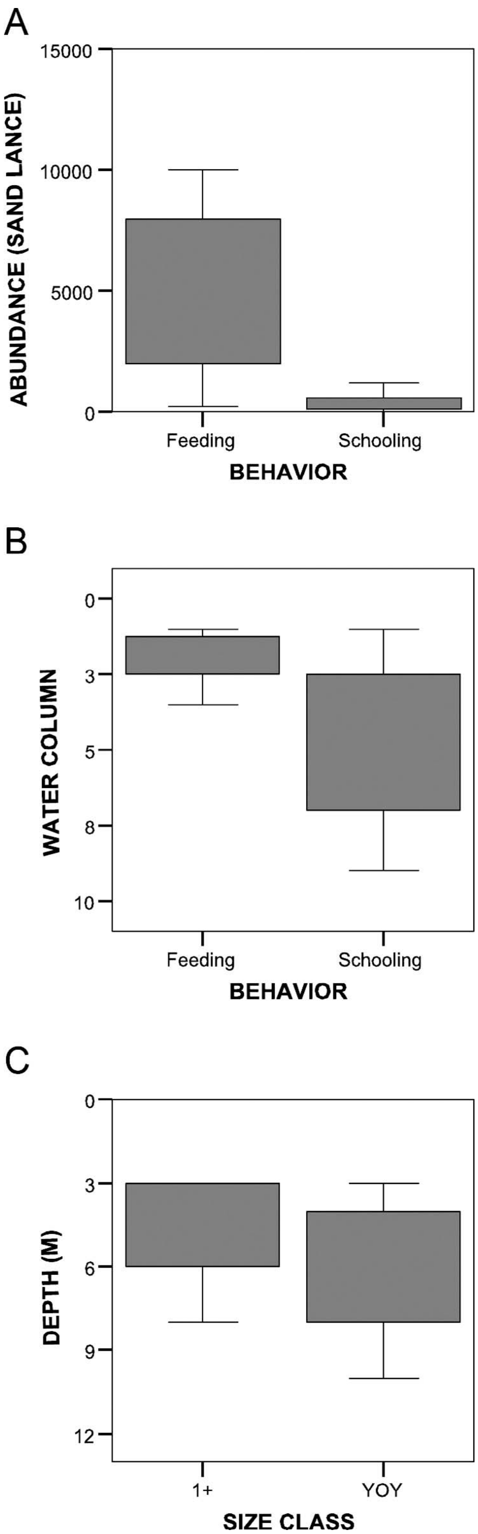
DISCUSSION

Intertidal Digging

Sand Lance were not found to bury themselves in beaches above the low tide mark within our study area as they have been found to do in nearby Barkley Sound (Haynes 2006), and in many other areas in their range (Dick and Warner 1982; Quinn 1999; Robards and others 1999). Comparison of the sediment properties showed that the intertidal sediment Particle Size Mean and Particle Sorting values for WCT beaches were similar to those at sites that had Sand Lance present in Barkley Sound (Haynes 2006). This suggests that differences in sediment characteristics do not explain the absence of intertidal burying on the WCT. Another possible explanation is the difference in shoreline exposure between the 2 study areas. High wave action disturbs sediment such that it would be less suitable for burying. Accessing the intertidal would require the Sand Lance to enter the high-energy zone where shore waves break on the beach. The Barkley Sound sites sampled by Haynes (2006) are much more sheltered than on the WCT. All WCT sites are highly exposed to the Pacific Ocean (Fig. 1) and have large wave heights due to swell generated offshore. Very few fish species can utilize turbulent surf zones of exposed shorelines (Layman 2000). It seems that frequent and intensive wave action precludes intertidal burying on the exposed WCT beaches even when sediments match those used elsewhere.

Sand Lance Presence-Absence

Sand Lance are known to remain close to sediment covered benthic areas or shorelines dominated by sediment (Ostrand and others 2005; Haynes 2006). In our study, the 4 sites with no sediment had no Sand Lance, reinforcing its importance as Sand Lance habitat. Models presented here not only stress the importance of sediment presence in determining habitat use in the shallow region of the subtidal but also the importance of sediment properties. The importance of sediment properties in determining habitat use in *Ammodytes* spp. has also been found for the intertidal region (*A.*



hexapterus, Haynes 2006) and for deeper subtidal regions (Lesser Sand-eel, *A. marinus*; Wright and others 2000; Holland and others 2005). In our logistic regression analysis the presence or absence of Sand Lance at 16 sites with some sediment were predicted with no classification error using 2 sediment variables (Particle Size Mean and Particle Sorting) and the interaction term. In the classification tree the 3 sediment variables also produced a model with no classification error for all 20 sites with or without Sand Lance, and showed the important thresholds for each independent variable and the hierarchical relationships between them (Fig. 3).

The subtidal Particle Size Mean was lower for sites with Sand Lance present than sites with Sand Lance absent. This is the opposite relationship to that found for intertidal substrates in Barkley Sound (Haynes 2006). This difference may arise because Sand Lance use subtidal and intertidal substrate types differently. If Sand Lance remain in the intertidal substrate above the tide line they are required to breathe the interstitial water. In this situation, sediment with smaller grain size would likely impede respiration. Subtidally, this may not be an issue as there would be more water available to a buried Sand Lance. Holland and others (2005) found that in the North Sea *A. marinus* selected subtidal burying sites characterized by medium or coarse sand (≥250 μm to <2 mm) or sites with a moderate level of fine gravel (≥2 to <8 mm) and avoided sites characterized by coarse gravel (≥8 mm), fine sand or silt (<250

←

FIGURE 5. Boxplots of significant behavioral relationships of Pacific Sand Lance (*Ammodytes hexapterus*): Behavior versus Abundance (A), Behavior versus Water Column (B), and Size Class versus Depth (C). The upper and lower quartiles are represented by the boxes, the median by the white line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values. Water Column y-axis represents the position in the water column of the Sand Lance with 0% representing the surface and 100% representing the seafloor. ''YOY'' represents young of the year size class (0-year) while ''1^+'' represents the 1^+-year size class (all other year classes). Note: outliers (>1.5 times the interquartile range from the median) were excluded from the plots.

μm), or sites with high or low levels of fine gravel. We found Sand Lance on the WCT at sites that had a Particle Size Mean ≤1290 μm, which falls within the range selected by *A. marinus,* but also includes 3 sites classified as fine sand (223, 228, and 238 μm) that *A. marinus* avoided and 3 sites just above the fine sand cut off (262, 275 and 296 μm). Selection for Particle Sorting on the WCT also differed from that found by Haynes (2006). Here, Sand Lance utilized areas with mixed sediments compared to Barkley Sound where Sand Lance used well-sorted sediments. This again may be due to differences in subtidal and intertidal habitat selection.

With a small dataset such as ours there is a danger of over-fitting and thus the strength of the relationships may have limited applicability. The logistic regression and classification tree have perfect classification suggesting that over-fitting may be the case. Evidence for over-fitting may be seen in the classification tree where Node 4 is split using Particle Sorting (Fig. 3). Although this split gives the model the perfect classification, the improvement is small relative to the other 2 splits. Also, cross-validation of the tree showed a higher misclassification of sites compared to re-substitution (15% cross-validation classification error compared to 0% for re-substitution), indicating that the model's perfect re-substitution performance is questionable.

Sand Lance Abundance

The regression tree explains a high degree of variance in the dataset, but the tree's ability to classify Sand Lance Abundance is limited. The tree has 3 terminal nodes (Nodes 1, 3, and 4, Fig. 4). Nodes 1 and 4 both had similarly low mean abundances (2.035 and 1.618 Sand Lance m^{-1}, respectively), while Node 3 had a high mean abundance (59.765 Sand Lance m^{-1}). This suggests that the model can accurately predict between high abundances and low abundances. However, Node 3 has only 2 cases, thus the model is useful in separating only those 2 cases of high abundance. This limited use suggests that the model may not be adequate in describing how habitat features affect the abundance of Sand Lance at sites. Although the model is untested as a predictive tool, it does indicate environmental factors such as particle size and sorting that are important for Sand Lance habitat use.

Behavioral Analysis

Sand Lance behavior likely affects their availability to marine predators (Hobson 1986). We identified 3 relationships in Sand Lance behavior that may in turn affect predator behavior:

1. Feeding Sand Lance appeared to aggregate in larger schools than those that were not feeding. This suggests that Sand Lance might alternate between larger foraging schools and smaller non-feeding schools. This is supported by the anecdotal evidence noted at Stanley's Beach (described above). This change in Sand Lance behavior and habitat use between the 2 surveys was only noted at 1 site, however, it suggests that kelp beds dominated by bedrock may be foraging habitat for Sand Lance. Schooling behavior is largely an anti-predator strategy (Seghers 1974). When feeding, Sand Lance may be more vulnerable and the safety benefits of forming large schools are likely more important. When they are not feeding, it may be beneficial to form smaller schools less easily detected by predators.

2. Feeding schools were generally found in mid-column water compared to non-feeding schools that remained closer to the seafloor. Sand Lance are visual feeders, preying primarily on copepods in the water column (O'Connell and Fives 1995). Because their prey are distributed within the water column, Sand Lance are required to frequent the mid-water column to feed. During periods when Sand Lance are not feeding it is probably advantageous to remain closer to the seafloor to be near the sediment in which to bury to avoid predators (Hobson 1986). Also, remaining close to the seafloor may allow Sand Lance to use cryptic coloration to blend in with the background sediment. In this situation the smaller non-feeding schools discussed above would be less conspicuous than the larger schools seen foraging.

3. Juvenile (0-year class) Sand Lance were found in deeper water than 1^{+}-year class Sand Lance. Although the difference was not great, this behavioral difference between size classes may play an important role in structuring foraging behavior of predators. Both Marbled Murrelets, *Brachyramphus marmoratus* (Carter 1984), and Rhinoceros Auklets, *Cerorhinca monocerata* (Davoren and Burger 1999) breeding

within our study area have been found to feed their chicks with 1+-year class Sand Lance while feeding themselves on the 0-year class. A segregation of size classes with depth, as suggested by these data, would affect foraging behavior. When Marbled Murrelets or Rhinoceros Auklets feed themselves in the nearshore regions close to beaches, they may frequent deeper waters to target 0-year class Sand Lance and when foraging for their chicks they may forage in slightly shallower waters. Juvenile Sand Lance off southwestern Vancouver Island are also found in near-surface balls in deeper water than we surveyed. Juvenile Sand Lance sometimes form mixed-species balls with juvenile herring and are often attacked by diving birds (Richards 1976; Davoren 2000; Davoren and Burger 1999). Mixed-species schools of Sand Lance, juvenile herring, and rockfish were noted in our surveys.

ACKNOWLEDGMENTS

The primary funding for this study came from a Science Horizons Grant (Environment Canada). Additional funding came from grants to AEB from the BC Forest Science Program, Endangered Species Recovery Fund (World Wildlife Fund Canada and Environment Canada) and NSERC Canada. Support for RAR was provided by a NSERC Canada Graduate Scholarship. We are extremely grateful to the Centre for Wildlife Ecology at Simon Fraser University (D Lank) and the Canadian Wildlife Service (D Bertram) for the loan of their rigid-hull inflatable and other equipment, to lightkeepers J and J Etzkorn, S Bell, S Harron, and C Martin for assistance with this research, and D Duffus for lending us the sediment grab. We thank N Watson for her field assistance. Thanks also to B Hansen and Parks Canada for their continued support of our research in Pacific Rim National Park. We thank Mark Zimmermann and an anonymous reviewer whose comments greatly improved this manuscript.

LITERATURE CITED

ABOOKIRE AA, PIATT JF. 2005. Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. Marine Ecology Progress Series 287:229–240.

ANTHONY JA, ROBY DD, TURCO KR. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248:53–78.

AVERY MI, SUDDABY D, INNES PME, SIM MW. 1992. Exceptionally low body weights of Arctic Terns *Sterna paradisaea* on Shetland. Ibis 134:87–88.

BLOTT SJ, PYE K. 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surface Processes and Landforms 26:1237–1248.

BREIMAN L, FRIEDMAN JL, OLSHEN RA, STONE CG. 1984. Classification and Regression Trees. Belmont, CA: Wadsworth International Group. 368 p.

CARTER HR. 1984. At-sea biology of the Marbled Murrelet (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia [thesis]. Winnipeg, Manitoba: University of Manitoba. 143 p.

DAVOREN GK. 2000. Variability in foraging in response to changing prey distributions in Rhinoceros Auklets. Marine Ecology Progress Series 198: 283–291.

DAVOREN GK, BURGER AE. 1999. Differences in prey selection and behavior during self-feeding and chick provisioning in Rhinoceros Auklets. Animal Behavior 58:853–863.

DICK MH, WARNER IM. 1982. Pacific Sand Lance, *Ammodytes hexapterus* Pallas, in the Kodiak Island group, Alaska. Syesis 15:43–50.

FIELD LJ. 1988. Pacific Sand Lance, *Ammodytes hexapterus*, with notes on related *Ammodytes* species. In: Wilimovsky NJ, Incze LC, Westrheim SJ, editors. Species synopses: life histories of selected fish and shellfish of the Northeast Pacific and Bering Sea. Seattle, WA: Washington Sea Grant Program and Fish Research Institute, University of Washington. p 15–33.

FOLK RL. 1974. Petrology of sedimentary rocks. Austin, TX: Hemphill Publishing Company. 182 p.

FOLK RL, WARD WC. 1957. Brazos River bar: a study in the significance of grain size parameters. Journal of Sedimentary Petrology 27:3–26.

HAMER KC, MONAGHAN P, UTTLEY JD, WALTON P, BURNS MD. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. Ibis 135:255–263.

HAYES DL, KULETZ KJ. 1997. Decline of Pigeon Guillemot populations in Prince William Sound, Alaska, and apparent changes in distribution and abundance of their prey. In: Baxter BR, editor. Forage Fishes in Marine Ecosystems. Fairbanks, AK: Alaska Sea Grant College Program, University of Alaska Fairbanks. p 699–702.

HAYNES TB. 2006. Modeling habitat use of young-of-the-year Pacific Sand Lance (*Ammodytes hexapterus*) in the nearshore region of Barkley Sound, British Columbia [thesis]. Victoria, BC: University of Victoria. 171 p.

HEDD A, BERTRAM DF, RYDER JL, JONES IL. 2006. Effects of interdecadal climate variability on marine trophic interactions: Rhinoceros Auklets and their fish prey. Marine Ecology Progress Series 309:263–278.

HOBSON ES. 1986. Predation on the Pacific Sand Lance, *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in Southeastern Alaska. Copeia 1986:223–226.

HOLLAND GJ, GREENSTREET SPR, GIBB IM, FRASER HM, ROBERTSON MR. 2005. Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment. Marine Ecology Progress Series 303:269–282.

HOLM S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

LAYMAN CA. 2000. Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia Barrier Islands. Estuarine, Coastal and Shelf Science 51:201–213.

LEWIS S, WANLESS S, WRIGHT PJ, HARRIS MP, BULL J, ELSTON DA. 2001. Diet and breeding performance of Black-legged Kittiwakes *Rissa tridactyla* at a North Sea colony. Marine Ecology Progress Series 221:277–284.

LITZOW MA, PIATT JF. 2003. Variance in prey abundance influences time budgets of breeding seabirds: evidence from Pigeon Guillemots *Cepphus columba.* Journal of Avian Biology 34:54–64.

LITZOW MA, PIATT JF, PRICHARD AK, ROBY DD. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286–295.

MARTIN AR. 1989. The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. Bird Study 36:170–180.

MOISEN GG, FRESCINO TS. 2002. Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling 157:209–225.

MONAGHAN P. 1992. Seabirds and sandeels: the conflict between exploitation and conservation in the northern North Sea. Biodiversity and Conservation 1:98–111.

NATIONAL BUOY DATA CENTER. 2007. Historical data. Stennis Space Center, MS: US Department of Commerce, National Oceanic and Atmospheric Administration, National Weather Service. Updated 14 June 2007, Cited 10 July 2007. Available from http://www.ndbc.noaa.gov/.

O'CONNELL M, FIVES JM. 1995. The biology of the Lesser Sand-eel *Ammodytes tobianus* I. in the Galway Bay area. Biology and Environment 95b:87–98.

OSTRAND WD, GOTTHARDT TA, HOWLIN S, ROBARDS MD. 2005. Habitat selection models for Pacific Sand Lance (*Ammodytes hexapterus*) in Prince William Sound, Alaska. Northwestern Naturalist 86: 131–143.

PINTO JM, PEARSON WH, ANDERSON JW. 1984. Sediment preferences and oil contamination in the Pacific Sand Lance *Ammodytes hexapterus.* Marine Biology 83:193–204.

QUINN T. 1999. Habitat characteristics of an intertidal aggregation of Pacific Sand Lance (*Ammodytes hexapterus*) at a north Puget Sound beach in Washington. Northwest Science 73:44–49.

RICHARDS SW. 1976. Mixed species schooling of postlarvae of *Ammodytes hexapterus* and *Clupea harengus harengus.* Journal of the Fisheries Research Board of Canada 33:843–844.

ROBARDS MD, ANTHONY JA, ROSE GA, PIATT JF. 1999. Changes in proximate composition and somatic energy content for Pacific Sand Lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. Journal of Experimental Marine Biology and Ecology 242:245–258.

ROBARDS MD, PIATT JF. 1999. Biology of the genus *Ammodytes*—the sand lances. In: Robards MD, Willson MF, Armstrong RH, Piatt JF, editors. Sand lance: a review of biology and predator relations and annotated bibliography. Portland, OR: Department of Agriculture, Forest Service, Pacific Northwest Research Station. p 1–16.

SEGHERS BH. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. Evolution 28:486–489.

SPRINGER AM, SPECKMAN SG. 1997. A forage fish is what? Summary of the symposium. In: Baxter BR, editor. Forage Fishes in Marine Ecosystems. Fairbanks, AK: Alaska Sea Grant College Program, University of Alaska Fairbanks. p 773–806.

SURYAN RM, IRONS DB, KAUFMAN M, BENSON J, JODICE PGR, ROBY DD, BROWN ED. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla.* Marine Ecology Progress Series 236:273–287.

UTTLEY J, MONAGHAN P, WHITE S. 1989. Differential effects of reduced sandeel availability on two sympatrically breeding species of tern. Ornis Scandinavica 20:273–277.

VERMEER K. 1979. Nesting requirements food and breeding distribution of Rhinoceros Auklets *Cerorhinca monocerata* and tufted puffins *Lunda cirrhata.* Ardea 67:101–110.

WILLSON MF, ARMSTRONG RH, ROBARDS MD, PIATT JF. 1999. Sand lance as cornerstone prey for predator populations. In: Robards MD, Willson MF, Armstrong RH, Piatt JF, editors. Sand lance: a review of biology and predator relations and annotated bibliography. Portland, OR: United States Department of Agriculture. p 17–38.

WRIGHT PJ, JENSEN H, TUCK I. 2000. The influence of sediment type on the distribution of the Lesser Sandeel, *Ammodytes marinus.* Journal of Sea Research 44:243–256.

Submitted 09 April 2007, accepted 13 July 2007. Corresponding Editor: JW Orr.