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

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ABSTRACT-- The Pacific sand lance (Ammodytes hexapterus) is an important prey species in the Pacific Northwest 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 $\leq 1290 \mu m$ and avoided mixed sediments (sorting values $< 3.09$ S.D.; 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.

Keywords: sand lance, Ammodytes hexapterus, habitat selection, schooling behavior, classification tree, southwest Vancouver Island.
INTRODUCTION

The genus *Ammodytes* is preyed upon by seabirds, marine mammals and piscivorous fishes throughout its range and is considered a critical link between zooplankton and top marine predators (Springer and Speckmann 1997; Willson and others 1999). *Ammodytes* species are highly efficient in the transfer of energy from the secondary producers to the 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). *Ammodytes* are prey to a large and diverse group of predators (see Willson and others 1999 for a review) and for many they are considered the primary prey item (for example Uttley and others 1994; Burkett 1995; Irons 1996). Variations in availability and distribution of *Ammodytes* species 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 is thought to be responsible for large scale breeding failure of numerous seabird species (Vermeer and others 1979; Martin 1989; Uttley and others 1989; Avery and others 1992; Hamer 1993; Hayes and Kuletz 1997).

Pacific sand lance (*A. hexapterus*) are abundant in nearshore regions of the Pacific Northwest, being found most commonly in water less than 50 m in depth (Robards and Piatt 1999). These small eel-like fish are considered epi-benthic, 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 conserve energy and avoid high levels of predation (Dick and Warner 1982; Quinn 1999). The burrowing behavior of sand lance causes it to be strongly tied to highly specific substrates of well drained coarse sand and small pebbles with mud and silt absent (Robards and Piatt 1999; 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).
On the southwest coast of Vancouver Island, the Pacific sand lance is an important prey item of many species including the threatened seabird, the Marbled Murrelet (*Brachyramphus marmoratus*). Overall, the Pacific sand lance is considered to be the most important food source for the murrelet across its range (Burkett 1995). Off southwestern Vancouver Island, Carter (1984) found that Pacific sand lance and juvenile Pacific herring (*Clupea harengus*) made up the majority of the murrelet’s diet. This dependency exemplifies how an understanding of sand lance ecology is necessary to further our understanding of predator habitat use and distribution for management purposes. In this study we examine the habitat use of juvenile and adult sand lance in the shallow subtidal region with regards to sediment properties (an important habitat requirement) and aspects of their behavior. Little is known about sand lance behavior, but their swimming, burrowing and foraging activities are likely to affect their availability to predators (Hobson 1986) and hence affect the distribution and foraging of predators.

**METHODS**

*Study Area*

The study was conducted between 29 May and 4 August 2006 within the West Coast Trail (WCT) unit of the Pacific Rim National Park Reserve of Canada on the west coast of Vancouver Island, British Columbia (Figure 1). We used the park boundary to delineate the study area which 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 outperform 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 attempted to sample all major beaches
(longer than 50 m) within the study area. Due to logistical constraints we could not sample all sites, but we estimated that we sampled 90% of all the major beaches within the study area (Figure 1). In addition, we surveyed 4 non-beach sites which 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, one along the ~4 m and one along the ~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. Observers recorded the abundance, behavior, fish size, depth and position in the water column of each sand lance aggregation. 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 using a ponar grab or by a snorkeler, and used for sediment 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 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.

For every 75 m of beach being sampled we dug a set of 5 pits. The pits were just above the tide line, approximately 8 m apart, and each pit was 1 m² 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.

_Sediment characteristics_
Subtidal sediment was first categorized by presence/absence (variable name: *Sediment Presence/Absence*) and incorporated in models as a binary variable (1/0 respectively). Samples from sites where subtidal sediment was present were processed using dry sieving techniques (Folk 1974). First, sediment was dried in an oven for 24 hours at 100°C. The samples were added to the top of a stack of 12 metal sieves ranging from 24,500 to 44 microns (µm). A mechanical shaker agitated the sieves for 15 minutes. 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 Mean Size* (microns) and *Particle Sorting* (S.D. 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 Mean Size* 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 Mean Size*, 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 sub-tidal 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 two dependent variables: *Sand lance Presence/Absence* and *Sand lance Abundance*. *Sand lance Presence/Absence* was coded as
Present (site has more than 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 (the minimum number of sand lance that were considered present was 4). *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, the mean abundance was used.

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 two, 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 three 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 analysis showed that sites with sediment absent had a perfect negative association with *Sand lance Presence/Absence*, *Sediment Presence/Absence* was forced as the first variable in the model.

The tree was validated using a V-fold cross-validation (Breiman and others 1984), which is one 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 from. After the growth had been terminated, the V-fold cross-validation prunes the tree by randomly partitioning the data into V groups (in this case ten) of equal or similar size. A classification tree of a specified size is built using nine of the ten groups and evaluated with the withheld group. This is done iteratively with each of the ten groups being withheld. This is repeated for each of the considered tree sizes starting with the terminal tree and continuing until the parent node is reached. The resulting ten cross-validation costs for each tree size can
be then 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 three independent variables. *Sediment Presence/Absence* was not forced as the first variable in this model.

**Behavioral Analysis**

Sand lance behavior was observed during the snorkeling surveys, and recorded in five categories: schooling (aggregated, moving as a group), feeding (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 streaming (schooling in a long narrow formation). We explored relationships between these behavior categories and five 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, <90mm), 1+ year (sand lance one year and older, >90mm). *Depth* was the recorded distance between seafloor and the surface of the water at the point which the 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 two categorical variables). We constructed a nonparametric correlation matrix to look for relationships among the 4 continuous variables.
RESULTS

We snorkeled over 38 km along 20 beach and 4 non-beach habitats. During these surveys we documented 151 sand lance aggregations. Sand lance were found on 57% of surveys at average 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, 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.

Intertidal digging

No sand lance were found in the intertidal digging surveys on the WCT (N = 150 pits dug at 30 points on 7 beaches). No significant differences were seen in the intertidal sediment characteristics found in the WCT compared to that found in Barkley Sound (Haynes 2006) using the Mann-Whitney U test (\( Particle Size Mean \) \( P = 0.198 \), \( Particle Sorting \) \( P = 0.102 \)). 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.

Sand lance Presence/Absence

Out of the 20 sites, 12 (60%) had sand lance present. We never found sand lance at the 4 sites without sediment (Table 1), and these sites were obviously excluded from analysis of sediment 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 revealed that sand lance presence or absence could be predicted by \( Particle Size Mean \), \( Particle Sorting \) and the interaction term \( Particle Size Mean \times Particle Sorting \) (Table 2). The logistic regression model had perfect classification with a pseudo r-squared value of 0.675, (2LL <0.001, model \( X^2 = 17.995 \), d.f. = 3, \( P < 0.001 \), Hosmer and Lemeshow goodness-of-fit test < 0.001, d.f. = 2, \( P = 1.00 \)). Further examination of independent variables showed that sites
with sand lance present had a lower Particle Size Mean and Particle Sorting than sites with sand lance absent (Figure 2). The classification tree had similar results showing perfect re-substitution classification (pure terminal nodes, Figure 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 sand lance are avoiding 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 S.D. with 4 of the 5 sites of the node having values less than this cut off (Node 5) and all 4 being sand lance absent sites. The remaining site had a value greater than 3.07 and had sand lance present (Node 6).

Cross-validation produced a risk estimate of 0.15 (S.E. 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 fewer than 0.5 sand lance per meter. 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 two splits with three terminal nodes, used two of the three independent variables in the analysis, and explained 99.4% of the variation in abundance (Figure 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 two 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 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, Figure 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. Water depth had no significant effect on feeding.

The two age classes (0 and 1+ year classes) showed a significant difference in water depth: the 0-class were found in deeper water (Table 3, Figure 5C). The age 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 were feeding versus schooling (P = 0.902). Spearman’s rank non-parametric correlation tests found 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 two 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 where all sites are highly exposed to the Pacific
Ocean (Figure 1). 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**

In a study of subtidal sand lance habitat, Ostrand and others (2005) found that sand lance remain close to areas of sediment. In our study, the 4 sites with no sediment had no sand lance, reinforcing the importance of sediment 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 sediment properties. The importance of sediment properties in determining habitat use has also been found for the intertidal region (Haynes 2006) and for deeper subtidal regions (Wright and others 2000; Holland and others 2005). In our logistic regression analysis, the presence or absence of sand lance at the remaining 16 sites with some sediment were predicted perfectly using the two sediment variables (*Particle Size Mean* and *Particle Sorting*) and the interaction term. In the classification tree, the three sediment variables also produced a perfect classification of all 20 sites with or without sand lance, and showed the important thresholds for each independent variable and the hierarchical relationships between them (Figure 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 µm) or sites with high or low levels of fine gravel. Sand lance here were found at sites that had a particle size mean ≤1290 µm which falls within the range of which *A. marinus* selected but also includes sites three sites classified as fine sand (223, 228, and 238 µm) which *A. marinus*
avoided and three sites just above the fine sand cut off (262, 275 and 296 μm). The selection for *Particle Sorting* on the WCT was similar to that found by Haynes (2006). In both areas sand lance were using well-sorted sediments and avoiding mixed sediment.

With a small dataset such as the one used in this study there is a danger of over-fitting with the data and thus the strength of the relationships may have limited applicability. The logistic regression and classification tree have perfect classification suggesting that overfitting may be the case. Evidence for overfitting may be seen in the classification tree where Node 4 is split using *Particle Sorting* (Figure 3). Although this split gives the model the perfect classification, the improvement is small relative to the other two 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 models 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 three terminal nodes (Nodes 1, 3, and 4, Figure 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 two cases thus the model is useful in separating only those two 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 the environmental factors (such as particle size and sorting) that are important for sand lance habitat use. This information is key in formulating theories and predictions regarding sand lance ecology.

### Behavioral Analysis

Sand lance behavior likely affects their availability to marine predators. We identified three relationships in sand lance behavior which may in turn affect predator behavior. First,
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 one site (Stanley’s). In the first survey at Stanley’s, 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 second 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 the kelp beds (*Nereocystis leutkeana*) further offshore, actively feeding in large dense schools in the upper half of the water column in an area not included in the original snorkel transects.

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.

Second, 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.

Third, juvenile (0-year class) sand lance were found in deeper water than 1+ sand lance. Although the difference was not great (Figure 6), it was statistically significant. This behavioral difference between size classes may play an important role in structuring foraging behavior of predators. Both Marbled Murrelets (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. If a segregation of size classes with regards to depth exists, as suggested by these data, then this would affect foraging behavior. When murrelets or 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). In our surveys, sand lance were noted to form mixed-species schools with juvenile herring and juvenile rockfish and also seen in balling formations.

It is important to consider that this study had a limited scope in examining sand lance behavior and therefore the results should be interpreted with care. Although we found significant relationships between behavioral variables, sand lance behavior is likely complex and therefore results may be oversimplified. Sand lance behavior is known to vary both spatially and temporally and is also affected by other variables not considered here (Field 1988; Robards and Piatt 1999). A more in-depth behavioral study on sand lance is required to verify the relationships found here.

This study describes key aspects of sand lance habitat use and behavior in the shallow subtidal region of the nearshore. As a key prey species, information on habitat use and behavior is essential for understanding the biology of sand lance as well as the biology of species that prey on sand lance. The distribution of sand lance is likely to affect to the distribution and reproductive success of predators (Willson and others 1999). Sand lance behavior described here likely plays an important role in structuring the foraging behavior of predators. In order to make better informed decisions regarding the management of marine predators and other marine resources, the ecology of sand lance should be considered and more thoroughly investigated.

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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$^{-1}$).

<table>
<thead>
<tr>
<th>Site</th>
<th>Late May</th>
<th>Late June</th>
<th>Early July</th>
<th>Late July</th>
<th>Early August</th>
<th>Change in Abundance</th>
<th>Consistency</th>
<th>Subtidal sediment P/A</th>
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<td>P</td>
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<td>Y</td>
<td>P</td>
<td></td>
<td></td>
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</tr>
<tr>
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<td>7.439</td>
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<tr>
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<td>A</td>
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</table>

*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 absence of sand lance at 16 sites with sediment present on the West Coast Trail.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>S.E.</th>
<th>Wald</th>
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<tr>
<td>Constant</td>
<td>682.6</td>
<td>14.9</td>
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<tr>
<td>Particle Size Mean</td>
<td>-0.4</td>
<td>42.3</td>
<td>&lt;0.001</td>
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<td>Particle Sorting</td>
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<tr>
<td>Particle Size Mean x Particle Sorting</td>
<td>692.7</td>
<td>65835.7</td>
<td>&lt;0.001</td>
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</table>

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
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+ size class (all other year classes).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Behavior</th>
<th>Mann-Whitney U</th>
<th>P-value</th>
<th>Size Class</th>
<th>Mean Rank</th>
<th>Mann-Whitney U</th>
<th>P-value</th>
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<tr>
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<tr>
<td>Schooling</td>
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<tr>
<td>Feeding</td>
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<tr>
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<td>Depth</td>
<td>Feeding</td>
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<td>YOY</td>
<td>58.9 [77]</td>
<td>626.5</td>
<td>0.001*</td>
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FIGURE CAPTIONS

FIGURE 1. Map of the study area and surrounding region.

FIGURE 2. Boxplots of the two quantitative sediment variables versus 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 (greater than three times the interquartile range from the median).

FIGURE 3. Classification tree for Sand lance Presence/Absence (0 = Absent, 1 = Present). Splits are created using the variable with the highest predictive power, maximizing the homogeneity of the two 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. The split of Node 0 (which contains all samples) was based on Sediment Presence/Absence (1/0 respectively) with all 4 sites with sediment absent also having sand lance absent (Node 2). Node 1 is further split by Particle Mean Size with all 11 sites having values < 1290 μm having sand lance present (Node 3). Node 4 was further split into two homogenous groups using a Particle Sorting value of 3.07 S.D. to separate the 1 sand lance present site (Node 6) from the 4 sand lance absent sites (Node 5).

FIGURE 4. Regression tree for Sand lance Abundance constructed using the three independent variables. “SORTING” represents Particle Sorting (S.D.) and “MEAN” represents Particle Size Mean (microns). “Improvement” refers to the decrease within-node variance (computed as the least-squared deviation). The tree’s use is limited as it only separates Node 3 which has a high mean sand lance abundance (only two sites) from Node 1 and 4 which have similar mean sand lance abundances.

FIGURE 5. Boxplots of significant behavioral relationships: Behavior versus Abundance (A), Behavior versus Water Column (B), 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 (in tenths) with 0 representing the surface and 10 representing the seafloor. “YOY” represents young of the year size class (0-year) while “1+” represents the 1+ year size class. Note: outliers (greater than 1.5 times the interquartile range from the median) were excluded from the plots.
Fig. 1.

- Barkley Sound
- Vancouver Island
- British Columbia
- Pacific Ocean

Legend:
- Snorkel
- Snorkel and Intertidal Digging
- Intertidal Digging

Map showing locations such as Bamfield, Cloose, and Camper Bay along the coastline of southwest Vancouver Island.
Fig. 2
Fig. 3.
Fig. 4
Fig. 5