



NOTE

Feeding Ecology of Pacific Sand Lance in the San Juan Archipelago

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Abstract

Forage fishes such as Pacific Sand Lance *Ammodytes personatus* are a crucial link between lower and upper elements in marine food webs, as they transfer energy from plankton to higher trophic levels. Despite their importance to marine food webs, little is known about the population structure and feeding ecology of Pacific Sand Lance. In this study, we examined the population density and diet composition of Pacific Sand Lance as well as feeding patterns and movement in response to tidal, diel, and seasonal cycles in a prominent sand wave field in the San Juan Channel, Washington. A generalized linear model was applied to account for the corresponding effects of tidal, diel, and seasonal trends as well as habitat affinity related to substrate type. We showed that fish distributions were predominantly driven by sediment type and that time of day had a significant influence on foraging behavior with distinct crepuscular feeding patterns. Our results also provide evidence for the cessation of feeding over the fall transition and the onset of a winter dormant period, as observed by increased densities of fish within the sand wave field (177%), a marked increase in the number of empty stomachs (511%), and a significant decrease in condition factor. These trends correspond with the expectations that Pacific Sand Lances exhibit a winter dormant phase and burrow in sediments throughout the winter months to conserve energy and reduce predation risk during periods of low productivity. We anticipate our study to be a starting point for understanding the foraging ecology of the Pacific Sand Lance, particularly in the San Juan Archipelago

and Salish Sea. The results of this study may improve the understanding of Pacific Sand Lance habitat and availability to pelagic predators, inform fisheries management, and increase the resolution of marine food web models.

The transfer of energy between primary and higher trophic levels in marine ecosystems often occurs through a few species of highly abundant, small forage fishes (Cury et al. 2000). As such, forage fishes are a crucial link between lower and upper elements in the food chain as they transfer energy from primary producers (e.g., phytoplankton) and secondary consumers (e.g., zooplankton) to higher trophic levels (e.g., piscivorous fishes, seabirds, and marine mammals) (Robards et al. 1998; Harvey et al. 2010). These fishes may also channel energy flow between various marine habitats, as many forage fish species occupy intertidal and subtidal communities (Robards et al. 1999). Variation in the abundance of forage fish populations can significantly impact marine ecosystems (Bargmann 1998). Thus, despite relatively few focused studies on these taxa, planktivorous fishes are an important component driving trophic dynamics in many marine and coastal ecosystems (Pikitch et al. 2012).

Subject editor: Kenneth Rose, University of Maryland Center for Environmental Science, Cambridge

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Received March 15, 2017; accepted August 9, 2017

The Pacific Sand Lance *Ammodytes personatus* (see Orr et al. 2015) is found along the west coast of the United States and Canada, as far north as the Arctic. While it is a valuable commercial stock in Japan and the North Sea, no fisheries exist in the northeastern Pacific Ocean except for occasional small bait fisheries in Washington and British Columbia (Trumble 1973). As in many unmanaged forage stocks, relatively few studies have focused on this species (Liedtke et al. 2013). Pacific Sand Lances are, however, an important component of marine food webs (Harwood and Croxall 1988; Gilman 1994; Bargmann 1998; Furness 2002; Penttila 2007) and a known food source to 45 species of commercial and sport fishes, 40 species of seabirds, and 12 species of marine mammals including threatened and endangered species (Field 1988; Robards et al. 1998; Harvey et al. 2010). While the Salish Sea is characterized by a large and diverse benthic community, some pelagic groups, including Pacific Sand Lance, account for relatively high rates of throughput, suggesting that they are more tightly coupled to overall energy flow in the system than are demersal groups and are indicators of important processes within the food web (Harvey et al. 2012) or of atmospheric conditions and climate patterns (Hipfner and Galbraith 2013). The importance of this fish to marine ecology is also apparent in the correlation between its abundance and predator populations; population declines have contributed to large-scale breeding failure in various seabird species (Wanless et al. 2005; Haynes et al. 2007).

Pacific Sand Lances are typically found in nearshore areas with coarse sand substrate (Greene et al. 2011). While spawning locations are well documented at beaches along the shoreline in the San Juan Islands and Puget Sound (Selleck et al. 2015), efforts to distinguish, map, and predict offshore benthic habitat is ongoing (Greene et al. 2011; M. R. Baker, unpublished data). Foraging is believed to occur predominantly at dawn and dusk (Hobson 1986; Robards et al. 1998; Wright et al. 2000). During the spring, summer, and fall, the species is considered epibenthic, and the fish forage in the pelagic environment for zooplankton prey and burrow in substrates to conserve energy and avoid predation (Field 1988; Robards et al. 1998; Haynes et al. 2007; Greene et al. 2011).

Anecdotal evidence suggests that in the winter Pacific Sand Lances enter a state of dormancy, remaining buried in the sediment for prolonged periods of time (Macer 1966; Fives 1967; Wright et al. 1998). Most investigators report that sand lances and sand eels are absent from the water column during winter months (Petersen 1977; Dick and Warner 1982; Field 1988) and appear inactive while buried in intertidal and subtidal substrates (Blackburn and Jackson 1980; O'Connell and Fives 1995; Robards et al. 2000). These fish are therefore not available to other marine taxa that rely on them as a food source in other times of the year. Although Pacific Sand Lances comprise a large part of the diet for most commercial fishes and marine birds and mammals in the Strait of Georgia and Puget Sound region, limited research exists on the feeding

ecology of this forage fish population (Field 1988; Washington Department of Fish and Wildlife 2016), particularly in regard to the fall season when they transition from summer foraging to winter dormancy. This research aims to (1) establish and quantify the diet composition of Pacific Sand Lance and (2) characterize feeding patterns and movement between benthic substrates and the pelagic environment, including the response of Pacific Sand Lances to tidal, diel, and seasonal drivers.

STUDY SITE

The Salish Sea (Juan de Fuca Strait, Puget Sound, and the Strait of Georgia, Washington and British Columbia) is a region defined by diverse bathymetry and strong tidal flow and supports diverse assemblages of marine consumers such as forage and commercial fishes, marine mammals, and seabirds (Thomson 1981; Lewis and Sharpe 1987). As an intersection and link between estuarine and oceanic influences within the Salish Sea, the San Juan Channel is the focus of a long-term monitoring study undertaken by the University of Washington. All samples relevant to this study were collected from the sand wave field in the San Juan Channel, a large glacial deposit of sediment that is 1.88 km in length and runs north (48°31.333'N, 122°57.083'W) to south (48°30.333'N, 122°57.167'W) in the middle of the channel. The sand wave is composed of nonuniform sediment, including silt, sand, gravel, and shell hash and covers an area of ~531,893 m² at a depth of 60–80 m (Greene et al. 2011; G. H. Greene, Seadoc Society, personal communication).

METHODS

Van Veen sediment grabs.—Pacific Sand Lances were sampled from unconsolidated sediment using a Van Veen grab sampler (0.12 m² of surface area per drop with a penetration depth of 22 cm). Camera-based experiments have shown sand lances buried to depths of 5 cm despite the presence of suitable sediment at greater depths (Gidmark et al. 2011). Samples were taken during eight cruises on the University of Washington RV *Centennial*, between September 28 and November 14, 2012. During each cruise, samples were taken from two locations on the north end of the sand wave, two locations in the central part, and two locations on the south end of the sand wave for a total of 43 successful grabs (Figure 1). Samples were also taken on the RV *Auklet* on three dates to fill in gaps in diel and tidal cycles. Grabs were counted if the Van Veen grab sampler successfully sealed and remained closed to retain sediment (e.g., did not latch onto large gravel or rocks on the bottom, which would prevent closure). Fish were euthanized with a lethal dose of tricaine methanesulfonate (MS-222) and fixed with 30 mL of buffered formalin to preserve each sample.

Mass, fork length, and population structure.—Mass and FL were taken for each individual fish. Mass was measured to the nearest 0.01 g by using a 400-g-capacity OHAUS Scout Pro

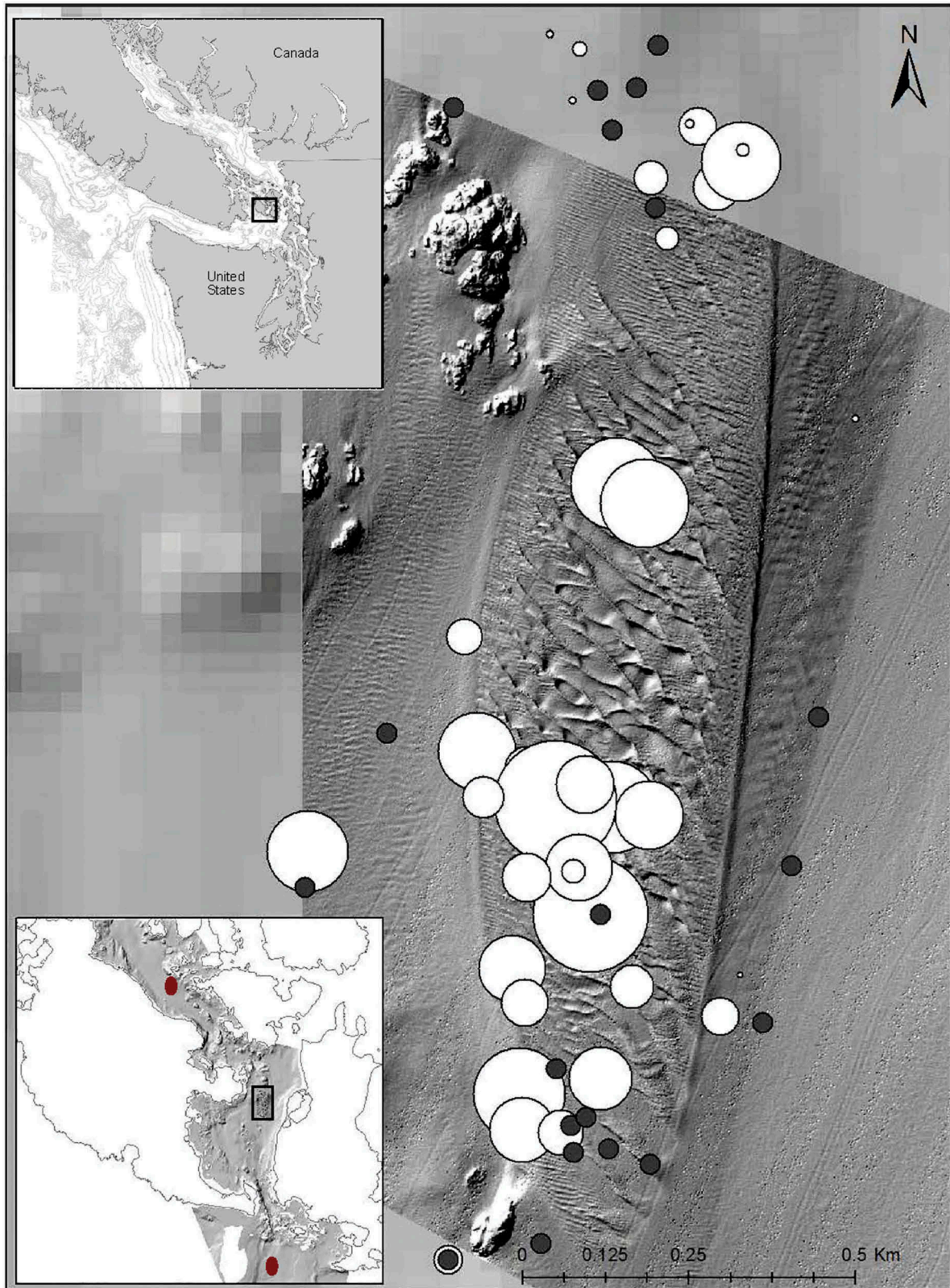


FIGURE 1. The sand wave field in the San Juan Channel and location of the Van Veen sediment grabs. The successful grabs (white circles) are scaled to the relative number of fish (CPUE). The unsuccessful grabs (dark circles) represent both incomplete grabs or grabs with no fish. The top inset map shows the full extent of the Salish Sea (west coast of United States and Canada) and the location of the San Juan Archipelago (outlined in black). The bottom inset map shows the bathymetry of the San Juan Channel, the location of the sand wave field in the San Juan Channel (outlined in black), and the location for north station and south station (dark red markers).

scale with a resolution of 0.01 g. Fork length was measured to the nearest whole millimeter. Age-at-length metrics were estimated according to length ranges associated with age-classes from the analyses of Pacific Sand Lance otoliths in this region, where fish under 65 mm were determined to be young of year (age 0), fish between 65 and 80 mm were assumed to be age 1, fish between 80 and 110 mm were assumed to be age 2, fish between 110 and 130 mm were assumed to be age 3, and fish between 130 and 150 mm were assumed to be age 4 (Greene et al. 2011; M. E. Matta, Alaska Fisheries Science Center, Age and Growth Laboratory, personal communication; T. Wylie-Echeverria, University of Washington, personal communication).

Condition factor.—Fulton's condition factor (K) was used to assess the energy reserves of fish through the course of the season (Fulton 1904; Ricker 1975). Fish that are heavy for their length have more energy reserves available for growth, reproduction, and survival during the winter dormant phase. Heincke (1908) established the usefulness of Fulton's condition factor for comparing seasonal changes in nutritional condition, and Clark (1928) explicitly correlated condition factor with fat content in forage fishes. Following recommendations on the analysis of weight-length relationships (Cone 1989; Murphy et al. 1991; Froese 2006), K was used for this within-population analysis rather than relative weight (W_r) (Wege and Anderson 1978), which is more appropriate for analyses across populations or species. Condition factor was calculated using the equation

$$K = 10^7 (W/L^3), \quad (1)$$

where W is weight in grams and L is FL in millimeters.

Stomach content analysis.—Grab samples taken on the same day were grouped together based on location within the sand wave. From each sample, five fish from each length class were randomly selected for stomach content analysis. Stomach fullness was assessed before excising the contents using a rank index of 0 (empty) to 4 (distended), and the digestion state was given a rank of 0 (not digested) to 4 (too digested to identify). Stomach contents were counted using a dissecting scope (Nikon SMZ645) and laboratory counters. Each organism was identified to the lowest taxonomic class possible. Analysis applied the frequency of occurrence (FO) method (proportion of stomachs containing each prey type was calculated and expressed as the percentage of the total number of stomachs) using the equation

$$\text{Diet}_i^{\text{FO}} = \frac{N_{\text{fish},i}}{N_{\text{fish}}} \cdot 100, \quad (2)$$

where N_{fish} is the total number of fish examined, $N_{\text{fish},i}$ is the number of fish with prey type i in their stomach.

Analyses also applied the numerical method (NM) (stomach contents of all fish in the sample were pooled and expressed as percentage of different prey types) by using the equation (Hyslop 1980; Ahlbeck et al. 2012)

$$\text{Diet}_i^{\text{NM2}} = \frac{\sum_{j=1}^{N_{\text{fish}}} N_{ij}}{\sum_{j=1}^{N_{\text{fish}}} N \cdot j} \cdot 100, \quad (3)$$

where $N \cdot j$ is the total number of prey in the stomach of fish j and N_{ij} is the number of prey type i in the stomach of fish j .

Zooplankton sampling.—Zooplankton samples were collected between September 28 and November 14, 2012, at two stations in San Juan Channel onboard the RV *Centennial*. The north station (48°35.00'N, 123°02.50'W) and the south station (48°25.20'N, 122°56.60'W) are roughly 10 km north and south, respectively, of the sand wave field in the San Juan Channel (Figure 1). Samples were collected by vertical tows from the University of Washington RV *Centennial* using a 70-cm-diameter, 153- μm -mesh net weighted at the cod end. The net was lowered to 10 m above the seafloor. The volume of each sample was calculated as

$$V = \pi r^2 \times l \quad (4)$$

where V is the tow volume, r is the radius of the net mouth, and l is the length of the tow.

Samples were fixed with 30 mL of buffered formalin and stored for future analysis. In the laboratory each sample was filtered through a 118- μm -mesh screen and rinsed with freshwater to remove formalin. The plankton were resuspended in freshwater and divided into two samples that were diluted by either one-half or one-quarter, depending on the perceived density, and then water was added to each dilution to obtain a final volume of 700 mL for enumeration. Two aliquots of 5 mL each were taken from each tow by means of a Stempel pipette and counted by using a square-gridded petri dish, a Nikon SMZ645 dissecting microscope, and laboratory counters. Each individual was identified to the lowest taxonomic level possible (T. P. Sigley, University of Washington, Friday Harbor Laboratories, unpublished).

Total densities for each taxon were calculated using the equation

$$D = \frac{[N \cdot s / (d \cdot a)]}{V}, \quad (5)$$

where D is the density of organisms for each taxon, N is the total count of organisms in the aliquot analyzed, s is the volume in milliliters of the divided sample, d is the dilution of the divided sample as a fraction of 1, a is the volume in milliliters of the aliquot analyzed, and V is the total volume of water sampled by the tow net, as calculated above (Sigley, unpublished).

Phytoplankton was sampled and analyzed in an analogous manner (G. M. Contolini, University of Washington, Friday Harbor Laboratories, unpublished).

To evaluate the influence of flood versus ebb tides, we evaluated zooplankton abundances at the south station collected 2007–2012 in the Friday Harbor Pelagic Ecosystem Function Research Apprenticeship (Sigley, unpublished). Zooplankton concentration values were transformed to the deviation from the annual mean concentration for that year. These concentrations were compared with the tidal direction of the preceding tide (ebb, flood) and tidal height, for late September to late November of each year from 2007 to 2012 at the National Oceanic and Atmospheric Administration (NOAA) weather station 9449880 located at the Friday Harbor Laboratories (<http://www.ndbc.noaa.gov/>).

Data on physical oceanographic processes and biological production.—Historical and present tide data were obtained from the NOAA Tides and Currents website (<http://tidesandcurrents.noaa.gov>). Tidal level was used for the Friday Harbor location (NOAA station number 9449880). Daily sea surface temperature (SST) and photosynthetically available radiation (PAR) measurements were secured from a location proximate to the south station via the NOAA National Data Buoy Center (station FRDW1-9449880) and evaluated in concert with fish densities and foraging data. Monthly measurements of SST, PAR, fluorescence, chlorophyll *a* concentrations, and net productivity of carbon were accessed via Aqua MODIS Net Primary Productivity (NOAA NMFS SWFSC ERD 2017a, 2017b, 2017c, 2017d, 2017e). These data were used to develop surface plots for comparison of in-season shifts in temperature, light, and production.

Statistical analysis.—Statistical analyses were run in R version 2.15 (R Core Team 2013) and graphical figures were developed in Sigma Plot 11.0. Chi-square tests were used to describe relationships between dependent variables (time of day and tide) to response variables (stomach fullness and digestive state). Linear regressions were conducted to determine the relationship between mean CPUE and condition factor as a function of season (calendar date). A generalized linear model (GLM) was developed to assess the interacting effects of time of day (diel cycle), tidal phase, season (calendar date), and sediment type (ϕ size, ϕ) on the abundance of Pacific Sand Lances in sampled substrates. Time of day was grouped into three categories: morning, afternoon, and evening. Morning was defined as 0700–1159 hours, afternoon was defined as 1200–1659 hours, and evening was defined as 1700–2100 hours. Generalized linear models extend linear modeling to scenarios that involve nonnormal error distributions and are useful in calculating deviance explained, determining patterns in the residuals, and identifying points with high leverage. Models are fit with an explicit probability density function using maximum likelihood approaches. In our analyses we considered Poisson and negative binomial error structures to account for overdispersion, which may result from sampling, aggregation

behavior, environmental variability, or a combination of factors. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. We therefore applied a negative binomial error structure in agreement with analyses of this type of data (Ver Hoef and Boveng 2007). We applied step-wise reduction to perform model simplification (backwards elimination from a maximal model).

RESULTS

A total of 1,032 Pacific Sand Lances were sampled in the San Juan Channel, and 155 specimens were used for stomach contents analysis. Fork length ranged from 23 to 137 mm, while weight ranged from 0.6 to 16.0 g.

Stomach Contents, Condition Factor, and Age Structure

Using the FO method (Figure 2), we determined unidentified copepods (55.2%) and unidentified organisms (62.1%) were present in Pacific Sand Lance diets the most often, followed by amphipods (48.3%), calanoid copepods (31.0%), *Coscinodiscus* sp. (13.8%), and polychaete worms (6.9%). In the numerical pooled analysis, unidentified copepods comprised 46.6% of the diet, followed by *Coscinodiscus* sp. (19.7%), calanoid copepods (16.9%), unidentified organisms (11.7%), amphipods (4.9%), and polychaete worms (0.3%). Using the numerical individual analysis method (Figure 3), unidentified copepods constituted 40.1% of the organisms in Pacific Sand Lance stomachs, followed by unidentified organisms (33.4%), calanoid copepods (16.7%), *Coscinodiscus* sp. (5.8%), amphipods (3.9%), and polychaete worms (0.1%). Of the 155 stomachs examined, 124 (80%) were empty (fullness = 0). Zooplankton tows identified calanoid copepods as the numerically dominant form of zooplankton in the water column (Figure 4).

The overall condition in fish declined as the season progressed ($R^2 = 0.04$, $P = 0.001$; Figure 5). An analysis of whether fish size or age-class shifted over the progression of the fall transition suggested that the age structure of the population remained constant throughout this period ($R^2 = 0.01$, $P = 0.001$; Figure 6).

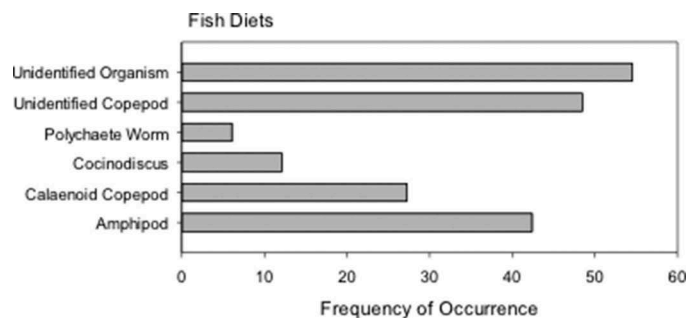


FIGURE 2. Pacific Sand Lance diets as a function of the frequency of occurrence method (proportion of fish stomachs with a particular organism).

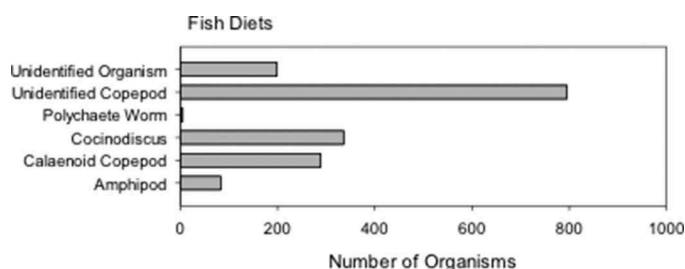


FIGURE 3. Pacific Sand Lance diets as a function of the numerical method (individual analysis of total number of organisms found in stomachs).

Patterns in Physical Oceanography, Primary Production, and Relative Density of Zooplankton

Both SST and PAR fell precipitously from October 8 through October 14 at the end of the first quarter of our sample time frame of September 28 through November 14 (Figure 7). Both phytoplankton and zooplankton counts also fell precipitously at a 2-d lag (October 10–17; Figure 7). Notable shifts in SST, PAR, chlorophyll *a*, fluorescence, and net production were also observed based on remote sensing data (Figure 8).

Copepods comprised the majority of sampled taxa in all zooplankton samples at both stations in the fall of 2012 (Figure 7). Adult calanoid and cyclopoid copepods and copepod nauplii together comprised 65–85% of the total zooplankton abundance in all samples (Mean = 72%, SD = 5.93, $N = 14$). Higher concentrations in planktonic copepods (*Calanoida* sp., *Cyclopoida* sp., *Harpacticoida* sp.) were noted on flood (deviation from the mean = 161 ± 992 SE, $N = 22$) versus ebb (deviation from the mean = -257 ± 298 SE, $N = 14$) tides at south station, but were not significant ($F_{1, 34} = 1.38$, $P = 0.247$). Tidal height was not a significant predictor of zooplankton concentrations within flood ($R^2 = 0.01$, $P = 0.832$) and ebb ($R^2 = 0.01$, $P = 0.149$) tides.

Stomach Fullness and Digestion

Patterns in stomach fullness (Figure 9) were influenced by time of day ($\chi^2 = 16.01$, $P = 0.042$) and date ($\chi^2 = 60.57$, $P = 0.019$) (Figure 9), but not digestion ($\chi^2 = 44.26$,

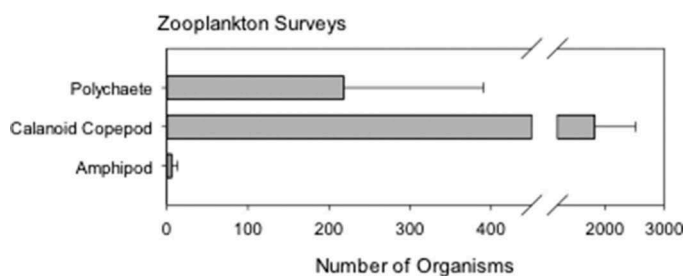


FIGURE 4. Results of zooplankton tows ($N = 7$) as a function of the density of organisms in the water column (total organisms within a standard sampled volume).

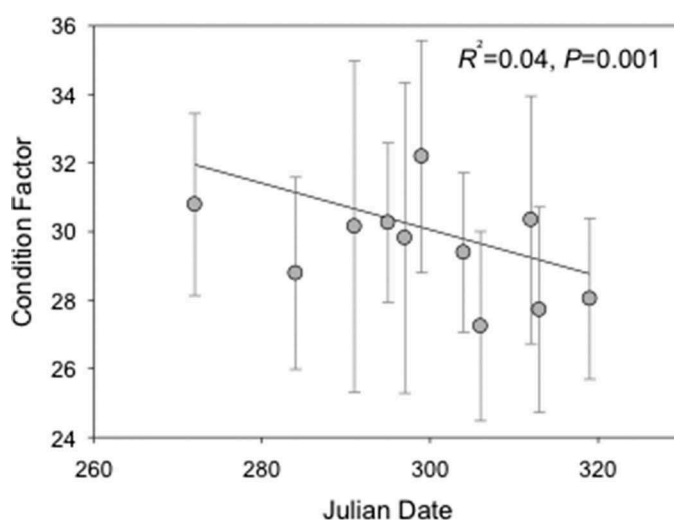


FIGURE 5. Condition factor (K , mean \pm SD) as a function (linear regression) of calendar (Julian) date (total fish sampled = 155).

$P = 0.045$). Tidal cycle appeared to influence foraging behavior but was not significant for either fullness ($\chi^2 = 17.17$, $P = 0.375$) (Figure 9) or digestion ($\chi^2 = 4.30$, $P = 0.828$). The mean stomach fullness (F) and digestive state (D) by age were highest for age-0 fish ($F = 0.69$, $D = 0.97$) and lowest for age-3 fish ($F = 0$, $D = 0$) (Figure 9). There was a significant relationship between stomach fullness and digestion ($\chi^2 = 19.56$, $P = 0.003$). Over the duration of the study the proportion of empty stomachs increased 511%.

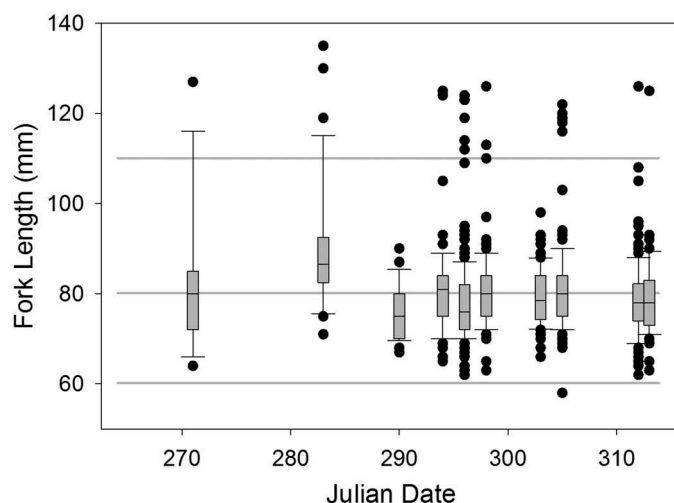


FIGURE 6. Length distributions of Pacific Sand Lances sampled throughout the fall season (total number of fish sampled = 155, length range of fish sampled = 58–137 mm). Horizontal lines mark the estimated breakpoint between age-classes, including age-0 to age-3 fish; fish less than 100 mm were assumed to be immature.

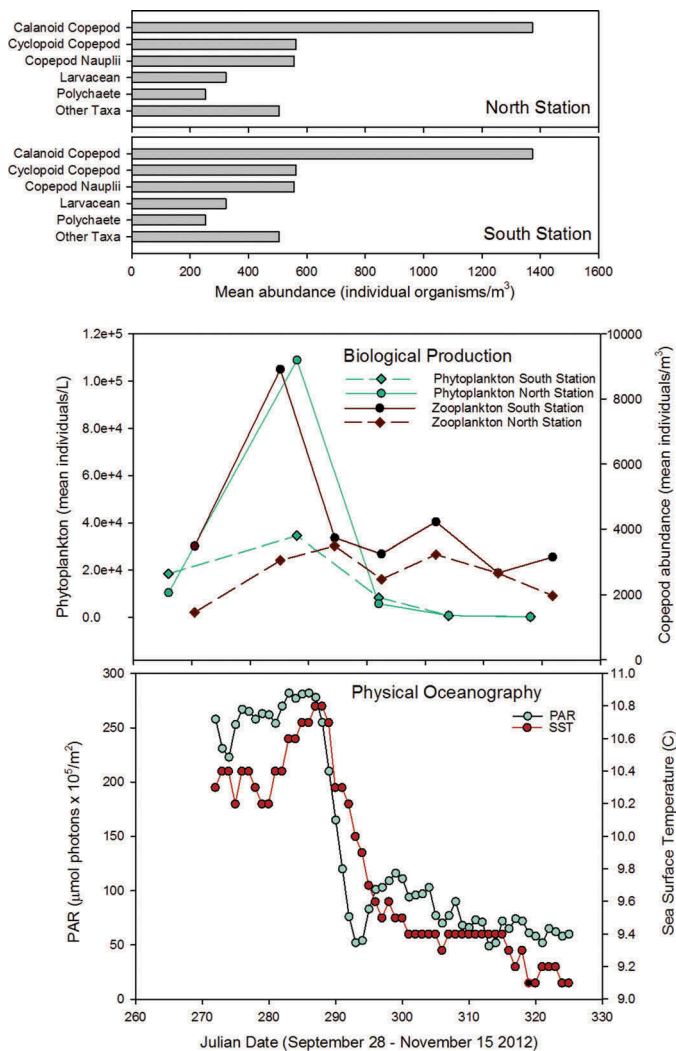


FIGURE 7. Relative proportions of taxa sampled in zooplankton tows at north station and south station, San Juan Channel, (bar graphs, top) and time series of physical oceanographic metrics and sampling related to primary and secondary production (scatter plots, bottom).

Model of Fish Densities and Residence in Surficial Sediments

A total of 1,032 fish were sampled over eight cruises with a total of 43 Van Veen grabs in the sand wave field in the San Juan Channel. The optimal explanatory model of Pacific Sand Lance density in the substrates of the San Juan Channel (GLM with negative binomial error structure) included sediment coarseness, date, time of day, and tidal phase, with an interaction term between date, time, and tidal phase to account for tidal phase and shifting daylight through the fall season. Starting with the maximal model we removed explanatory variables through stepwise regression. On the basis of Akaike's information criterion (AIC), we retained all terms in the model (Tables 1, 2). Accounting for multiple explanatory variables, we determined that the

presence of coarse sediment was the dominant factor determining Pacific Sand Lance densities within the sand wave field (mean CPUE, $z = 3.67$, $P < 0.000$). Date was not significant ($z = 0.74$, $P = 0.462$), though mean densities increased over the course of the fall (Figure 10). Time of day was also not significant in isolation ($z = 0.90$, $P = 0.367$); however, fish densities in the sand wave field were lowest at dawn and dusk. The influence of tidal regime (e.g., slack, flood, ebb) and velocity (e.g., slow, fast, maximum) was significant in isolation (maximum flood: $z = 2.92$, $P = 0.004$; fast flood: $z = 2.45$, $P = 0.014$) and as an interaction with time of day (maximum flood: $z = -2.98$, $P = 0.002$; fast flood: $z = -2.16$, $P = 0.031$), such that fish were found in higher densities in the sediments during flood tides, indicating an avoidance of the pelagic environment during these conditions (Figure 10). Pacific Sand Lance densities were highest in the center of the sand wave where the sediment type was predominantly coarse sand ($\phi = 0-1$ mm) (Wentworth 1922).

Population Estimate

Based on the mean CPUE ($N_{\text{mean fish per sample}} = 24$) over all successful samples throughout the season ($N_{\text{samples}} = 43$), the sampling surface area of the Van Veen grab sampler (0.12 m^2), and the estimated planar area of the sand wave field ($531,893 \text{ m}^2$) we estimated there were approximately 100 million Pacific Sand Lances in the sand wave field in the San Juan Channel in the fall of 2012.

DISCUSSION

Planktivorous forage fishes are key components responsible for the energy transfer from primary producers and consumers to piscivorous fish such as salmon and higher order predators such as marine mammals and seabirds. In the San Juan Channel, Pacific Sand Lances are especially important in structuring nearshore marine predator-prey interactions and food web dynamics (Zamon 2003).

Abundance and Benthic Habitat

This study confirms the presence of large numbers of Pacific Sand Lances within coarse grain sediments at a depth of 60–80 m. We propose a crude minimum regional abundance estimate of 100 million Pacific Sand Lances in the sand wave field in the San Juan Channel on the basis of repeated sampling during the fall 2012. Continuous refinement of this figure is needed to replicate these analyses, as well as the consideration of other sand wave fields in the area (Greene et al. 2011). Sand Lances are known to be abundant in nearshore areas ranging in depth to 100 m (Reay 1970; Field 1988; Boulcott et al. 2007). The large abundance and regular presence of Pacific Sand Lances in benthic habitats at 80 m (Baker, unpublished data) as well as documented remotely operated vehicle observations of Pacific Sand Lances in this

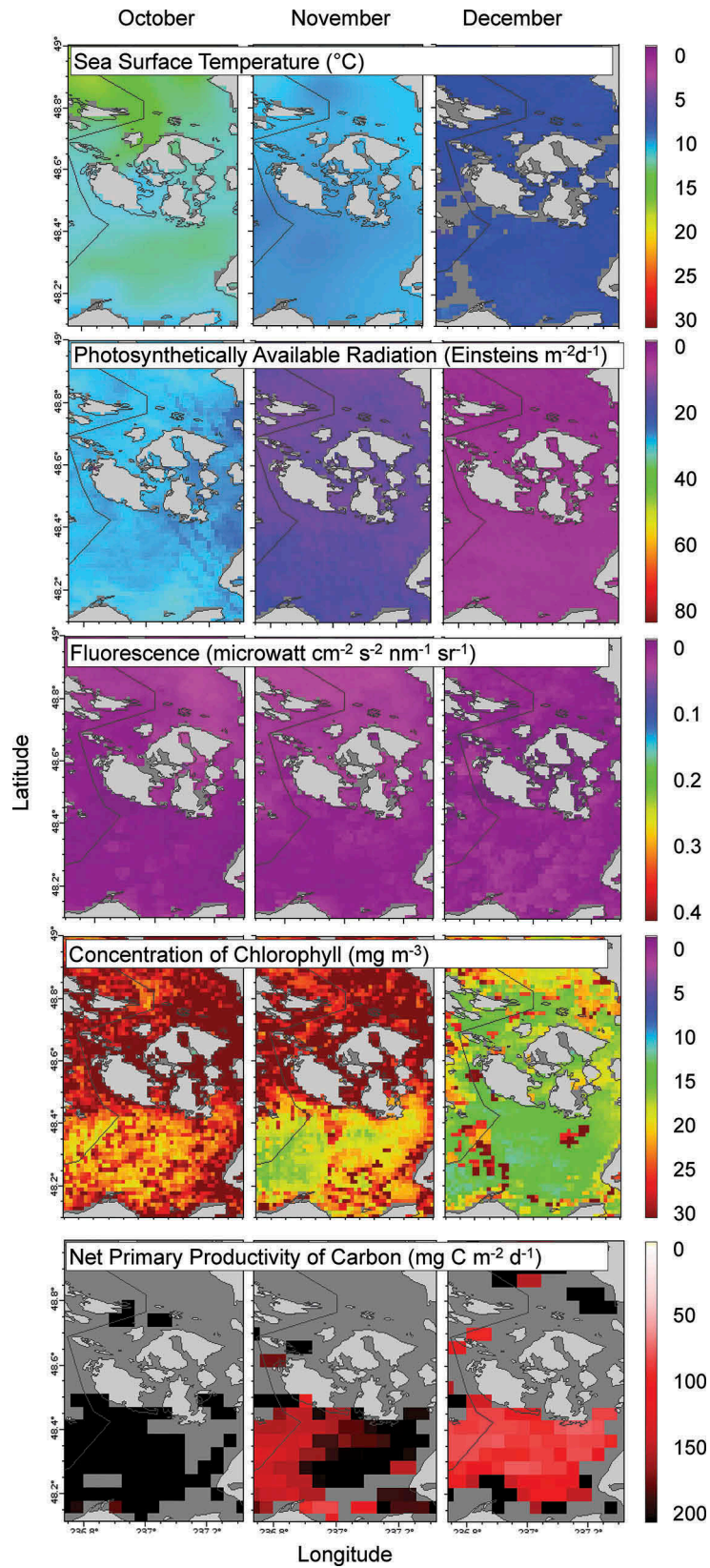


FIGURE 8. Physical oceanographic and biological productivity indices derived via NOAA National Data Buoy Center and Aqua MODIS Net Primary Productivity.

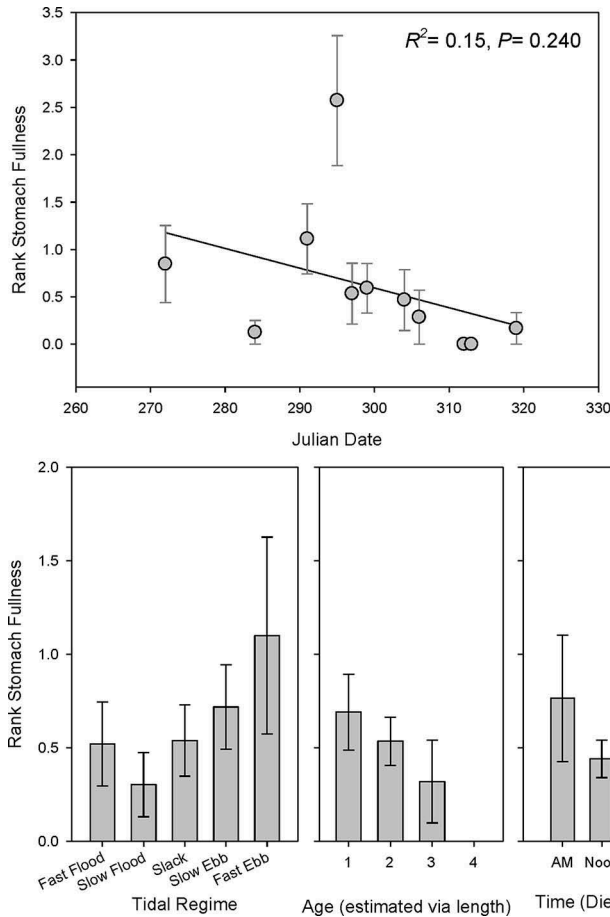


FIGURE 9. Ranked stomach fullness (mean ± SE) in Pacific Sand Lances and its relation to season (calendar [Julian] date), tidal regime, age (years), and diel cycle (time of day).

region at a depth of 280 m (D. Lowry, Washington Department of Fish and Wildlife, personal communication) suggest that recently proposed benthic habitat models for Pacific Sand

TABLE 1. Results and diagnostics for the generalized linear models (negative binomial error structure) of Pacific Sand Lance density (CPUE) in the substrates of the sand wave field in the San Juan Channel. The best-fitting model (first row) included sediment coarseness and the interaction of date, time of day, and tidal phase as explanatory variables.

Model	Equivalent df	ΔAIC
Sediment + date × time × tide	19	
Sediment	2	1.0915
Sediment + date	3	2.3896
Sediment + time	3	2.7164
Sediment + date × time	5	5.9792
Sediment + date + time × tide	14	6.7664
Sediment + tide	7	7.2051
Sediment + time + tide + date	9	7.2382
Sediment + time + tide	8	8.1343
Date	2	9.4614
Time	2	11.3933
Time + date	3	11.4552
Tide + date	7	17.6307
Tide	6	17.8543
Time + tide + date	8	19.3573
Time + tide	7	19.7509

Lances based on the assumption they are found to a maximum depth range of 60 m (Ostrand et al. 2005; Robinson et al. 2013) should be revised. Pacific Sand Lances may be able to utilize benthic sediments at depths far exceeding 100 m.

Diet Composition

The major food items found in Pacific Sand Lances sampled in the sand wave field in the San Juan Channel were consistent with plankton tow data throughout fall 2012; these results indicate that Pacific Sand Lances are opportunistic feeders. As in other studies on *Ammodytes* species, copepods were found to be the dominant taxon in the diets (Macer

TABLE 2. Analysis of deviance for model variables. The diagnostics for the best-fitting model are as follows: dispersion parameter for the negative binomial = 7.982, null deviance = 120.83 on 40 df, and residual deviance = 42.067 on 22 df; $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$.

Variable	df	Deviance	Residual df	Residual deviance	P (χ)
Null			40	120.83	
Sediment	1	26.84	39	93.99	$2.21 \times 10^{-7}^{***}$
Date	1	0.87	38	93.12	0.351
Time	1	1.55	37	91.56	0.212
Tide	5	12.53	32	79.03	0.028*
Date × time	1	0.10	31	78.93	0.752
Date × tide	2	3.11	29	75.82	0.211
Time × tide	5	20.39	24	55.43	0.001**
Date × time × tide	2	13.36	22	42.07	0.001**

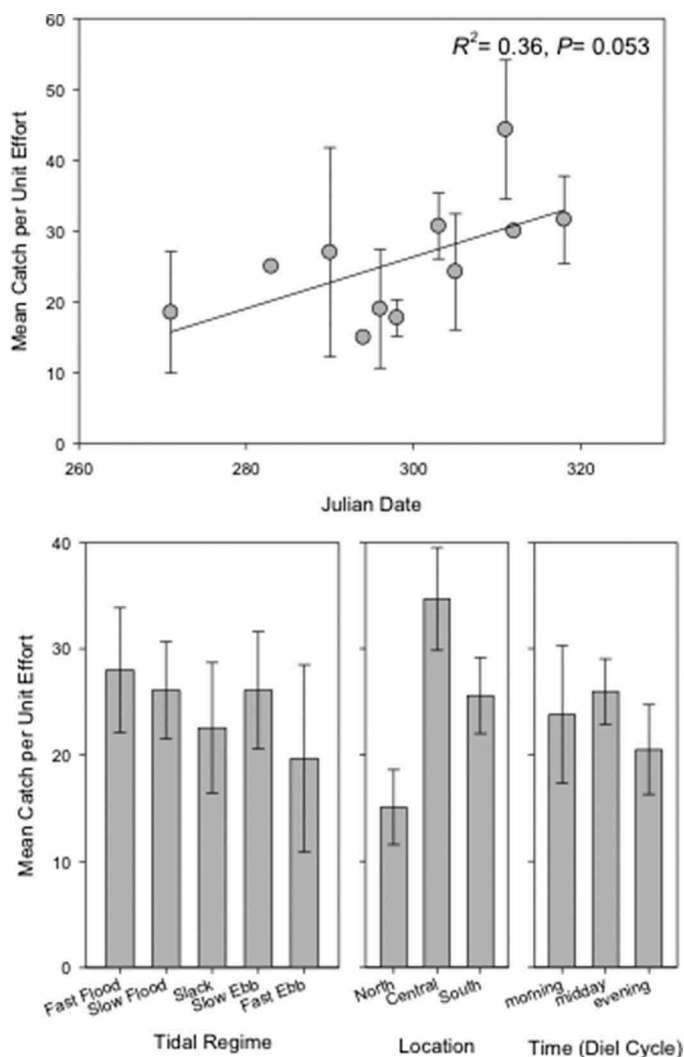


FIGURE 10. Mean density abundance (CPUE, mean \pm SE) of Pacific Sand Lances in sampled sediments as a function (linear regression) of season (calendar [Julian] date) and its relation to tidal regime, diel cycle (time of day), and location within the sand wave field in the San Juan Channel.

1966; Hipfner and Galbraith 2014). The suite of prey taxa observed in our studies is similar to that of other species of sand lances, including Northern Sand Lance *A. dubius* (Scott 1973) and American Sand Lance *A. americanus* (Meyer et al. 1979; Richards 1982), and is similar to Pacific Sand Lances analyzed at other locations (Sekiguchi 1977; Field 1988; Blackburn and Anderson 1997; Robards et al. 1999; Hipfner and Galbraith 2013) and within the region (Hipfner and Galbraith 2014).

Response to Tidal Activity and Diel Trends

Due to our sampling method, abundance estimates characterized dormant phases rather than actively foraging ones for Pacific Sand Lances. We inferred that periods of lower abundance in sediment suggested elevated activity in the

water column. Vertical movements between benthic substrates and the pelagic environment are likely related to active foraging forays and predation avoidance (Robards et al. 1999). On the basis of underwater observations, Hobson (1986) reported that some Pacific Sand Lances were buried in the sand at all times of the day but many were feeding in the upper water column. Our results demonstrated shifts in the relative density of Pacific Sand Lances in benthic substrates over the course of the day, where fish are more actively foraging in the pelagic environment at dawn and dusk, and higher rates of dormant burrowing behavior occurred during midday. Stomach fullness was also highest in the morning and evening. Furthermore, stomach analyses suggest that time of day has a significant influence on stomach fullness but not digestion. While active foraging and schooling may occur throughout the day, it appears that pelagic activity increases in periods of low light (i.e., crepuscular behavior). The euphotic zone in the inland waters of the Pacific Northwest is between 0 and 30 m (the true euphotic zone, defined by the depth at which light intensity falls to 1% of surface levels, varies from 10 to 100 m in PAR data collected by conductivity, temperature, and depth measurements in the Juan de Fuca Strait and Eddy Region; NOAA Fisheries NWFS and Puget Sound Institute 2012; Davis et al. 2014). Therefore, Pacific Sand Lances that use this particular sand wave field in daylight hours are not only protected by the sediment but also by darkness, thus deterring visual predators.

Our results also suggest tidal exchange and velocity are important. Copepods, the primary source of prey for sand lances, are significantly more abundant in the southern region of the San Juan Channel during flood tides than during ebb tides (Zamon 2002; Sigley, personal communication). Despite the higher abundance of zooplankton prey resources during flood tides, our results suggest Pacific Sand Lances exhibited high rates of dormancy during flood tides. Pacific Sand Lance abundance in sediment was lowest and stomach fullness was highest during ebb tides, suggesting foraging was higher during this tidal phase. Foraging may reflect a complicated set of tradeoffs aimed at maximizing foraging efficiency on the basis of prey availability, while simultaneously minimizing relative energy expenditures and predation risk, given tidal phase and velocity (Ahrens et al. 2012).

Trends across the Fall Transition

Over the course of the fall season, fish densities within substrates progressively increased while stomach fullness and digestive state decreased in Pacific Sand Lances. Together this provides support for the initiation of a winter dormant phase.

Regular periodic sampling of the sand wave field in the San Juan Channel indicates densities of Pacific Sand Lances in these sediments increase from July to October (Greene et al. 2011) and throughout October and November (Baker, unpublished data), indicating overwinter behavior. Studies of the Pacific Sand Lance in the pelagic environment have observed

corresponding trends (Robards et al. 1999), such that Pacific Sand Lances are rarely found in the water column during winter months. Pacific Sand Lances in this region are known to spawn between December and February in intertidal habitats (Penttila 1995), and Lesser Sand Eels *A. marinus* can migrate between deep and nearshore waters as a function of season and life stage (Andriyashev 1954; Gauld 1990); however, the lack of differentiation of the size-classes of fish sampled suggest that the increased abundance in the sediments represents a transition from pelagic foraging to benthic dormancy rather than an influx in the return of spawning adults. Additionally, while *Ammodytes* species mature at various ages across their range (Robards and Piatt 1999), and size at maturity is not known for the local population (Selleck et al. 2015), maturation does not occur until fish exceed 100 mm in length (Boulcott et al. 2007). Despite close examination of more than 1,000 individuals we noted no evidence of sexual maturation. Moreover, Pacific Sand Lances associated with spawning typically range from 170 to 190 mm in length (Selleck et al. 2015), whereas the maximum length of fish sampled in our study was 137 mm.

We found a weak but significant inverse relationship between stomach fullness and fish density (CPUE) as a function of diel and tidal cycles, suggesting that increased abundance within substrate is an indication that Pacific Sand Lances are dormant while within the sediment.

Our observations provide insight to the onset of winter dormancy, a phase assumed to occur November–March with re-emergence in April (Winslade 1974c). The accumulation of sufficient fat reserves as well as decreasing light, temperature, and available prey resources may all be important factors in determining the timing of the onset of dormant behavior (Winslade 1974a, 1974b, 1974c; Girsu and Danilov 1978).

Implications

Our study was designed to further understand the foraging ecology of Pacific Sand Lance in the context of a seasonal shift from summer foraging to winter dormancy. There are extremely limited data and insights to this important transition phase. While many studies have also suggested that Pacific Sand Lances may enter a dormant phase in winter, most statements are based on speculation or inferred from the absence of Pacific Sand Lances in acoustic assessments or net hauls. Few studies have provided concrete evidence for this shift in diets or in foraging behavior. Fewer still have provided data across the fall transition from the summer production period (i.e., upwelling and extended photoperiod) to winter (i.e., downwelling and light limited). By examining stomachs and densities of fish in the sediments across this transition period our study provides evidence for the onset of winter dormancy as well as its timing in this region.

Qualifying Assumptions

We recognize that these results encompass only one season and characterize a population with a limited age composition. Also due to our sampling methods, our vantage point is from the perspective of presence within substrates rather than within the water column. The use of pelagic habitats by Pacific Sand Lances remains largely unknown. A combination of simultaneous midwater and surface trawls, acoustic surveys, and sediment sampling would be valuable to better characterize habitat use and the feeding ecology of Pacific Sand Lances. Coordinated efforts to integrate these approaches are planned in Alaska (NOAA, National Marine Fisheries Service) and in the Salish Sea (University of Washington, Friday Harbor Laboratories, Seadoc Society).

Future studies should incorporate seasonal surveying of the sand wave field in the San Juan Channel and other similar benthic habitats in nearshore areas to better inform how patterns in Pacific Sand Lance abundance, distribution, and age composition shift within annual and seasonal scales. Additionally, finer scale sampling over tidal and diel cycles would improve the understanding of their feeding behavior. Proper aging of Pacific Sand Lances in this system via otolith or scale analyses would also add important information regarding the population structure of the southern range of the species. Also, maximum length may vary among populations; Robards et al. (1999) showed that lengths for Pacific Sand Lances in the Gulf of Alaska and California Current was abbreviated (maximum length = 200 mm) compared with those in the Bering Sea (maximum length = 270 mm). Expanding analyses to include other sand fields in the San Juan Archipelago would also increase understanding of habitat preference and provide a better estimate of Pacific Sand Lance abundance in the region.

ACKNOWLEDGMENTS

We thank J. Newton, B. Tyler, and R. McLaughlin for their assistance and continued support. We also thank and acknowledge G. Greene and J. Aschoff for the use of multibeam graphic images of the sand wave in the San Juan Channel and assistance with geospatial analysis, T. Sigley for analysis of zooplankton samples, B. Matta for insight on age–length estimates and otolith analysis, A. Summers and J. Bizzarro for their professional expertise and insight on sediment association, and T. Wyllie-Echevvera and M. Rood for their insights and historical perspective. We also thank K. Rose as well as three anonymous reviewers for their recommendations and advice to improve our manuscript. We are particularly appreciative of the considerable contributions of D. Willows and W. Krieger of the RV *Centennial* and colleagues in the 2012 Pelagic Ecosystem Function apprenticeship, particularly C. Heller and A. Thomson, as well as the those from the community of the Friday Harbor Lab for their assistance throughout the course of this study and analysis.

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