Spatiotemporal variation in Pacific sand lance (*Ammodytes hexpaterus*) abundance and demographics in the San Juan Channel

Olivia J. Graham[1]

Pelagic Ecosystem Function (PEF) Research Apprenticeship

Fall 2014

[1]Friday Harbor Laboratories, University of Washington, Friday Harbor, WA 98250

Contact information:
Olivia Graham
ojgraham@mac.com

Keywords: Pacific sand lance, *Ammodytes hexapterus*, diel behavior, antipredation window, year class strength, match/mismatch hypothesis, catch per unit effort, condition factor

Abstract

Fish feeding behavior, abundance, and population demographics depend on a number of environmental and non-environmental factors. Some fish, such as salmonids, display cyclic population structures and year class strength that are independent of their environment (Selbie 2008), whereas other fish are strongly influenced by light (Friedlaender et al. 2009), temperature (Cowx and Frear 2004) and tides (Witt 2011). Pacific sand lance (*Ammodytes hexapterus*) exhibited potential cyclic structures in previous studies, making them ideal for this abundance and population demographic study. Sand lance were collected from the San Juan archipelago and were examined to determine within-day, seasonal, and inter-annual patterns between: foraging behavior and light, time, and tides; abundance (catch per unit effort, CPUE), condition (condition factor, K), and age group structures. Together, these data suggest that sand lance foraging behavior is influenced tidal heights, although greater resolution is needed to determine the effects of other environmental conditions. Across larger temporal scales, local sand lance populations were in much lower condition that in previous years, suggesting the fall of 2014 had unusual environmental conditions. Finally, the sand lance exhibited a cyclic population structure with regards to year class strength, although not in abundance patterns. Further studies in sand lance abundance and population demographics would be useful to confirm this pattern.

Introduction

Many fishes' feeding behaviors depend upon different abiotic and biotic factors, ranging from prey availability to tides (Melnikov et al. 1981, Clark and Levy 1988). Of these factors, light can be a particularly important determinant of feeding behavior. For example, rainbow smelt and juvenile sockeye salmon diel movements frequently correspond to light intensities in the water column; they feed during an "antipredation window" in which moderate light levels illuminate their prey without exposing themselves to predators (Appenzeller and Leggett 1995, Clark and Levy 1988). Another species that exhibits diel behavior is the Pacific sand lance, *Ammodytes hexapterus,* which feeds in dense schools at dawn and dusk and burrows in sediment during daylight hours (Robards et al. 1999, Friedlaender et al 2009). However, it is unknown whether sand lance feed within an antipredation window.

Pacific sand lance (PSL), *Ammodytes hexapterus*, are small fish found throughout cold coastal waters worldwide (Robards et al. 1999). They are known for their high lipid content (Robards et al. 1999), and are a key food source for many marine birds, mammals, and other fish species (Geiger 1987). Because sand lance are vital linkages between marine trophic levels that connect plankton to larger predators, they can serve as indicators of the overall health of their ecosystems (Robards et al. 1999).

The abundance and age group structures of a fish population can serve as indicators for the population's overall state or condition. Certain fish species, such as Pacific salmon, exhibit fluctuating patterns of abundance that vary annually and are independent of environmental factors (Selbie 2008). Inter-annual changes in abundance may also be explained by the "match mismatch hypothesis," which suggests that the timing of larval fish growth and prey abundance strongly influence larval development, survival, and ultimately recruitment the following year (Bollens et al. 1992; Fortier, Ponton and Gilbert 1995).

The timing of periods of larval growth and variable plankton blooms affects the size of certain fish age groups in a given year, known as year class strength (Bollens et al. 1992; Haldorson et al. 1993; Fortier, Ponton and Gilbert 1995). Previous studies with Pacific sand lance (Haldorson et al. 1989, 1993), haddock (Cushings and Horwood 1994), American shad (Crecco and Savoy 1984), and walleye pollock (Bailey et al. 1995) indicate that year class strengths are directly related to larval feeding success. In years where there was a match between larval growth periods and plankton blooms, the resulting increases in zooplankton abundance led to greater larval fish growth, survival, and strong populations of year one fish the following year (Crecco and Savoy 1984, Haldorsen et al. 1989, Haldorsen et al. 1993, Cushings and Horwood 1994, Bailey et al. 1995). Within the San Juan archipelago, previous sand lance studies suggest that sand lance may exhibit a cyclic population structure as indicated by year class strength (Blaine 2006, Rood 2010, Greene et al. 2011, Witt 2011, Heller 2012, Pham 2013).

This study aimed to determine the abundance and population demographics of Pacific sand lance across daily, seasonal, and annual temporal scales in the San Juan Channel. To do so, the first part of the study examined sand lance abundance with respect to different light intensities, time, and tidal regimes to detect within-day behavioral patterns. The second part of the study aimed to define the San Juan Channel sand wave field and Jackson Beach sand lance populations for the fall 2014 season with respect to abundance (indicated by catch per unit effort, CPUE), condition factor (K), and age. Finally, these findings were compared to previous years' data to determine if local populations exhibit a cyclic population structure or inter-annual differences.

Methods and Materials

The San Juan Channel is a well-established spawning area and habitat for sand lance, as it has sandy beaches that are ideal for spawning and benthic habitats for burrowing (Greene et al. 2011, Washington State Department of Ecology). Although sand lance were only recently discovered in the San Juan Channel sand wave field (Blaine 2006, Greene et al. 2011), they have been known to spawn along sandy beaches throughout the San Juan Archipelago for many years (Geiger 1987, Washington State

Department of Ecology). In particular, Jackson Beach is a well-documented spawning beach (Washington State Department of Ecology; Figure 1) and the San Juan Channel sand wave field has an estimated population of over 44,000 sand lance (Blaine 2006, Greene et al. 2011).

Sand lance were collected from Jackson Beach and the San Juan Channel sand wave field. To determine feeding behaviors and the population demographics of the two populations, two distinct methods were employed. At Jackson Beach, a nylon mesh net that measured 36.6 m in length and 3.7 m in depth was used for beach seines. A total of 24 seines were conducted between September 29-October 29 at dawn (n=5), midday (n=2), and dusk (n=17). Seines were performed across different tidal heights and cycles, from which 165 sand lance were collected. All sand lance were included in the analyses.

To catch sand lance swimming in the water column, one end of the seine net was held upright at the water's edge. While the motoring the *Auklet* or the *Coot*, FHL small watercrafts, in a U-shape perpendicular to the beach, the remainder of the seine net was deposited into the water, while the other end was held and used to pull the seine net in to shore. Any and all sand lance caught were anesthetized using a 1:1 ratio of MS-222 and baking soda (to buffer to solution) then preserved using buffered formalin (formaldehyde supersaturated with Borax), which was added 10 minutes after the final gill movement. All other species were released. For most seines, the following were recorded: seine number, time, and the number of sand lance. For the few seining events that did not have all of the sampling data (9/29, 10/30), the sampling times and number of seines were estimated.

Van Veen grabs were conducted off of the *R/V Centennial* and the *Auklet* from September 30-November 10. Of the total 86 grabs performed, 66 closed completely. Across almost all of the San Juan Channel sampling events, sample areas were targeted to those in the San Juan Channel sand wave field that had historically complete grabs of 10 or more fish (Baker, personal communication). These areas were navigated to using the Navionics iPhone application. The only event that did not directly targeted these areas was the 3rd Centennial cruise (10/14), since these samples were intended to determine new sand lance habitats. Van Veen grabs were also attempted at Jackson Beach on a single sample day, but all grabs only contained mud, suggesting that they were performed too far offshore.

Once at the sampling site, a Van Veen grab was deployed and its contents (of up to 0.12 m^2) were emptied into large tubs. Sand lance were collected, anaesthetized, and returned to the lab for further analyses. For each grab performed, the following were recorded: grab number, depth, time, number of sand lance, complete/incomplete status, and the coordinates. Grabs were identified as "incomplete" if the Van Veen was not completely closed and was obstructed by a rock, piece of wood, or other debris. Only fish from complete grabs were analyzed (n=586), as incomplete grabs did not provide accurate representations of the sand lance in the area.

The sand lance were counted and measured in a hood. For each fish, the following measurements were taken: the fork length (FL), total length, width (behind the pectoral fins, across the girdle), the wet weight and the dry weight after the fish was allowed to dry at ambient temperature for approximately 4 hours. All length measurements were taken using a caliper and were measured to the nearest half-millimeter. The weights were measured using an electronic scale and were reported to the nearest hundredth-gram.

The fork lengths were used to approximate the age of the sand lance and were based on Wylie-Echeverria's length-age categories (unpublished data 2010): 0-69 mm (Year 0), 70-109 (Year 1), 110-129 (Year 2), and 130-150 (Year 3). Condition factor, K, was calculated using the following formula from Rood (2010), where m is the fish mass (g) and L is the fork length (mm):

$$K = m * 10^7 * L^{-3}$$

The catch per unit effort (CPUE) was determined as the number of sand lance in each seine or grab:

$$CPUE = \text{total PSL caught/seine or grab}$$

Several web-based resources were used to gather environmental measurements. Light measurements were originally measured using a light meter off at the time each seine was conducted, but due to equipment malfunctions, all atmospheric light measurements were collected from the Friday Harbor Weather Station at times most similar to the actual sampling time (Northwest Association of Networked Ocean Observing Systems (NANOOS)). The tidal heights and cycles for each sampling event were determined using online tidal charts for Friday Harbor (Pentcheff). Times for dawn and dusk in Friday Harbor were collected using the Sunrise, Sunset iPhone application, and were used to calculate the minimum time deviation from dawn or dusk and the time of the seining event.

Historical data were used from four sand lance studies performed in the San Juan archipelago, including catch per unit efforts (Heller 2012, Pham 2013), condition factors (Heller 2012, Pham 2013), and fork length measurements (Rood 2010, Witt 2011, Heller 2012, Pham 2013). Sediment sizes (phi sizes) for San Juan Channel sediment samples were taken from Bynum's study and were used for one analysis (2014).

Results

Part I: Within-day Foraging Patterns

The light and abundance data indicated that the number of sand lance caught at Jackson Beach increased with ambient light measurements until a given point, after which the number of sand lance decreased (Figure 2). Although these data matched the predicted pattern, there was not a detectable significant relationship between light and sand lance caught (R^2=0.1101, p=0.2939). The San Juan Channel data were also consistent with the anticipated pattern and did not exhibit a significant effect (R^2=0.0001, p=0.9977; Figure 3). In both cases, the data were fit to a nonspecific functional relationship using a polynomial equation to indicate the shape of the data.

The deviation from dawn or dusk and sampling time did not have a significant effect on the number of sand lance caught at Jackson Beach nor in the San Juan Channel. Furthermore, neither the dawn nor the dusk data sets were consistent predicted Poisson distributions. The highest number of sand lance were expected to be concentrated around dawn and dusk and to gradually reduce with increases in time. When the data from dawn samples at Jackson Beach were plotted together, they were found not to have a significant effect (R^2=0.1822, p=0.8178; Figure 4). Likewise, there was not a detectable significant relationship between minimum time from dusk and the number of sand lance caught (R^2=0.2216, p=0.1348; Figure 5). The number of sand lance caught in the San Juan Channel did not exhibit a significant relationship with time (R^2=0.0078, p=0.4876; figure not shown).

A two-way ANOVA was performed to determine if there was an effect of tidal heights, tidal cycles, or an interaction effect on the number of sand lance caught at Jackson Beach. Tidal height was found to have a significant effect (F_1=11.99, p=0.041), although neither tidal cycles nor the interaction between heights and cycles significantly influenced the number of sand lance caught (tidal cycle: F_1=9.06, p=0.057; interaction: F_1=6.094, p=0.0902; Figure 6).

A general linear model was used to determine whether and how tidal height, tidal cycle, and sediment size (phi size) influenced the number of sand lance caught in the San Juan Channel. None of the factors were found to significantly affect the number of sand lance caught (tidal height: F_1=0.052, p=0.82; tidal cycle: F_1=1.10, p=0.29; interaction: F_1=1.72, p=0.196; Figure 7).

Part II: Seasonal and Inter-annual Patterns

The San Juan Channel mean CPUE increased over the fall 2014 season, although not significantly (R^2=0.1795, p=0.2558; Figure 8). The CPUE for fall 2014 San Juan Channel sand lance was moderately higher than the CPUE from the previous fall (Figure 10). Across the 2012-2014 fall seasons, the highest mean CPUE occurred in 2012 and subsequently declined in 2013 and 2014.

Unlike the seasonal increase in CPUE for San Juan Channel sand lance, the Jackson Beach mean CPUE for the fall 2014 season did not change significantly across the season ($R^2=1.09*10^{-5}$, p=0.9944; Figure 9). When compared to inter-annual CPUEs from Jackson Beach, this fall's mean CPUE was considerably lower than the 2013 median CPUE (14 and 85 fish/grab; Figure 11). Across the 2012-2014 fall seasons at Jackson Beach, the highest abundance occurred in 2012 and declined in subsequent years, with 2014 having the lowest recorded abundance.

For the fall 2014 season, the sand lance in the San Juan Channel were in better condition than those at Jackson Beach, as reflected by their larger condition factors (Figure 12). In comparison to the condition factors from the fall of 2012 and 2013, this fall's sand lance had the lowest condition factors (Figure 13). Sand lance from the fall of 2013 displayed the highest condition factors (Pham 2013).

This fall, the sand lance from Jackson Beach and the San Juan Channel were largely dominated by year 1 fish (Figure 14). Similarly, the other even years also strong year class strength, wherein the populations were predominantly year one fish, with slightly more young of the year (YOY) fish from Jackson Beach as well (Rood 2010, Sisson 2012). This pattern contrasts sharply with the odd years that had higher proportions of older, year two and year three sand lance than in even years (Pham 2013, Witt 2011). Finally, both within the fall 2014 season and in comparison to previous years, San Juan Channel sand lance were consistently larger and older than Jackson Beach sand lance (Figure 15).

Discussion

Although there was not a significant effect of light on the number of sand lance caught, the data from Jackson Beach fit the anticipated pattern (Figure 2). According to the antipredation window hypothesis, there is a moderate range of light levels that allow fish to forage without experiencing high predation; beyond this narrow window, ambient light conditions are either insufficient for foraging or may increase predation risk (Appenzeller and Leggett 1995, Clark and Levy 1988). The Jackson Beach data fit this predicted curve, as there was a gradual increase in the number of sand lance caught as ambient light levels increased before tapering off. The weak relationship could be due to the lack of sampling efforts at moderate light levels between 125-225 PAR, where the fitted curve indicates the highest abundance would be. Also, one of the most abundant seines (n=78 fish) was conducted in very low light levels, rather than in moderate levels as anticipated.

Because the San Juan Channel grabs were taken between depths of 55-97 meters where there was no detectable light (NANOOS), it was presumed that light would not influence sand lance feeding behavior in the San Juan Channel. The data reflected this, as there was neither a detectable pattern in the fit line nor significant statistical results (Figure 3).

The lack of a significant relationship between the time of dawn sampling and the number of sand lance caught at Jackson Beach could be due to the low sample size (n=5 seines). Fewer dawn seines were conducted than dusk seines, and a greater amount of data across both times could better indicate a pattern, if there is one. In comparison, a total of 19 dusk seines were completed, which provided better data resolution and a slightly less insignificant effect (p=0.1348). However, multiple seines with low yields (n=0-1 fish) created considerable noise, making it difficult to ascertain if there were significant fluctuations in abundance over time.

The significant effect of tidal height on the number of sand lance collected at Jackson Beach could be attributed to the fact that lower tides reduce the distance sand lance must travel to forage. Because sand lance swim at relatively slow speeds, traveling to distant foraging areas is energetically costly and involves high predation risk (Engelhard 2008). By foraging at low tides when sand lance do not have to swim as close to shore as they do when foraging at high tides, sand lance could reduce energetic costs and their chances of being predated.

Unlike the numbers of sand lance collected at Jackson Beach, those collected in the San Juan Channel were not significantly influenced by tides or sediment size. Since Jackson Beach is smaller and shallower than the Channel sand wave field, it is logical that tidal height would not have a significant influence in the Channel, where changes in tidal height are not as noticeable. Additionally, unequal sample sizes may have compromised the analyses, as there were not any grabs performed at low slack tides in the San Juan Channel (Figure7). Finally, it is likely that the lack of data contrast (not having the sediment phi size for complete grabs with zero fish) influenced the results. Because sand lance are known to select for coarse sand over other types of sediment (Bynum 2014), it is probable that a complete set of phi sizes for sediment grabs with and without sand lance (rather than only those with sand lance) would exhibit a significant effect on the number of sand lance caught.

The increase in the San Juan Channel CPUE for the fall of 2014 is consistent with predictions and with previous findings (Figure 8; Heller 2012, Sisson 2012). From late October to early November, sand lance burrow into the sediment and enter their winter dormancy (Robards et al. 1999). Because increasing numbers of sand lance enter dormancy as the fall season progresses, it was expected that there would be more abundant grabs collected later in the fall season. This is precisely what the data indicate, although there was not a significant relationship between Julian date and CPUE. The insignificant effect could be due to the fact that the final sampling efforts—namely the final three sampling dates—yielded low catches. Likewise, the third and fourth sampling days (10/14 and 10/21) had remarkably low CPUEs, which may not be representative of the actual abundance.

The grabs conducted on the third sampling date were largely targeted at historically unsampled areas, leading to very few complete grabs. In contrast, most other sampling events targeted historically successful areas, and yielded higher numbers of complete grabs with sand lance. Although the grabs conducted on the fourth cruise were targeted at areas that had historically high abundance (over 10 sand lance per grab, Baker personal communication), few complete grabs were taken, as the majority of the grabs were rocky and incomplete. Based on the fall 2014 CPUE, it is likely that the winter dormancy for sand lance in the San Juan Channel began in late October or early November, as this was where there was an increase in the number of sand lance caught (i.e. increase in sand lance caught in the sediment).

Unlike the San Juan Channel mean CPUE for the fall of 2014, the Jackson Beach CPUE did not exhibit a distinct pattern across time (Figure 9). Due to the timing of sand lances' dormancy period, it was expected that there would have been a steady decrease in the number of sand lance caught at Jackson Beach, since fewer fish would be feeding and swimming in the water column later in the season. This pattern was supported by Pham's CPUEs from Jackson Beach (2013), although data from this fall season did not support this pattern. This could be due to the fact that the fifth sample event, which was late in the season, yielded the highest catch per unit effort, while it should have been one of the lowest (Figure 9). Another potential explanation for the low sample sizes and resulting insignificant CPUE could be attributed to the sampling method. A previous study on sand lance distribution in Alaska suggested that low sampling efforts (i.e., seines with zero sand lance) and their schooling behavior could account for some variability in the catches (Johnson et al. 2008). Because sand lance are schooling fish, it is difficult for seines to accurately represent fish populations, since there is considerable variability depending on whether or not schools of sand lance are caught. From the fall 2014 data, the winter dormancy for the Jackson Beach sand lance can be inferred to have started earlier than in the San Juan Channel, since there were remarkably fewer sand lance caught after the fifth sampling day. The condition of sand lance in the San Juan Channel reflects this difference in dormancy timing between the two populations.

Neither the San Juan Channel nor the Jackson Beach inter-annual CPUEs supported the anticipated cyclic population structure, since there was only a small increases in abundance in the San Juan Channel (Figure 10) and a decrease in abundance at Jackson Beach (Figure 11). Although the respective abundances did not support the cyclic pattern, the age groups corroborated a cyclic pattern of year class strength.

The San Juan Channel sand lance may have been in slightly better condition than those at Jackson Beach, since they were larger and older (Figure 14). In comparison to the Jackson Beach sand lance, those from the San Juan Channel were consistently bigger than those at Jackson Beach. Naturally, these older fish would be in better condition than younger, smaller fish that tend to dominate the Jackson Beach population (Rood 2010, Heller 2012, Pham 2013). However, the fall 2014 sand lance had greatly reduced condition factors than in previous years, which could be due to different environmental factors this year (Figure 13).

The fall 2014 season was marked by unusual environmental conditions that may be reflected by the condition of Pacific sand lance. Other local marine species, such as Harbor porpoises (*Phocoena phocoena*) had the lowest abundance in several years (Hayes 2014). Likewise, the overall avian biomass observed this fall was lower than in previous years, suggestive of different conditions than in previous years, such as warmer ocean temperatures (Barton 2014). Sea surface temperatures in and around the Salish Sea were considerably warmer this fall than in previous fall seasons, partially due to the anomalous warm water "blob" in Gulf of Alaska (Cougan 2014). Previous studies indicated that variations in water temperatures significantly influenced annual variations in year class strength in freshwater fish and salmon species (Mills and Mann 1985, Cowx and Frear 2004). Because temperature can be an influential factor in determining fish larvae growth and survival, it is possible that the increased surface temperatures this fall compromised sand lance growth, survival, and recruitment.

A mismatch in timing between plankton blooms and the key periods of sand lance larval growth may also account for the lower conditions in the fall 2014 season. Sand lance are considered early strategists, as their periods of growth are such that they coincide with peak copepod abundance (Haldorson et al. 1989, Bollens et al. 1992, Haldorsen et al. 1993). The timing of these events is particularly important for developing fish larvae, as studies have shown that year class strength is directly related to larval fishes' feeding success and zooplankton density (Crecco and Savoy 1984, Cushings and Horwood 1994, Fortier et al. 1995). If environmental conditions are such that plankton blooms occur earlier or later than critical growth periods—either in the spring for larval development or in the late winter when adults emerge from dormancy (Robards et al. 1999)—then fish growth and survival that year can be compromised. For the fall 2014 season, sand lance collected from the San Juan Channel and Jackson Beach exhibited reduced conditions that were reflected in their age class structures.

The distinct age class structures observed in both the San Juan Channel and Jackson Beach populations provide evidence that there is a cyclic pattern to the sand lance age groups. Overall, the past five fall seasons' age group structures indicate that sand lance have alternating populations of younger and older fish in even and odd years, respectively (Figure 15). Even years clearly display a large pulse of young fish, whereas even years have larger proportions of older fish. The fact that few young of the year (YOY) fish were collected from Jackson Beach and the San Juan Channel this fall is consistent with the low conditions and low abundances.

The smaller, younger populations of sand lance at Jackson Beach found this year and in previous years are consistent with prior findings, since Jackson Beach is a known spawning area and habitat for young sand lance (Washington State Department of Ecology). Similarly, the somewhat larger, older sand lance in the San Juan Channel found this season were consistent with those from earlier studies, suggesting that the San Juan Channel can support a large population of young sand lance (Blaine 2006, Rood 2010, Witt 2011, Heller 2012, Pham 2013, Greene et al. 2011). However, because few mature sand lance—those over two years of age—have been found in the San Juan Channel and at Jackson Beach over the past five years (Figure 15), it is possible that these local populations may use Jackson Beach and the San Juan Channel wave field for spawning and rearing grounds before relocating to other habitats once they mature (Robards et al. 1999, Witt 2011).

Moving to another habitat would be costly for sand lance, given their small size, slow swimming speeds and high chance of predation (Engelhard 2008). However, former studies provide evidence that year two and three sand lance may relocate to other areas in the San Juan Archipelago (Ewings 2011, Greene et al. 2011, Witt 2011). From example, although the San Juan Channel sand lance population has been historically dominated by immature, year one sand lance, those discovered in a sand wave field south of Suica Island were largely mature (Witt 2011). These findings suggest that sand lance in the San Juan archipelago utilize different habitats at different stages of their lives.

This study enhanced the growing body of knowledge about Pacific sand lance in the San Juan Channel (Blaine 2006, Rood 2010, Greene et al. 2011, Witt 2011, Heller 2012, Sisson 2012, Pham 2013). Future studies could further develop several or all of the aspects investigated in this analysis to further understand sand lance foraging patterns, abundance, and demographics.

In the future, studies that involve beach seines would likely benefit from seining in rapid succession, as sand lance abundance appeared to change rapidly in the several minutes between seines (Figures 4 and 5). Doing would possibly provide higher data resolution (i.e. more seines with greater variance in sand lance caught), thereby allowing any patterns between abundance and light and time to be more clearly determined. Furthermore, other light studies could utilize a light meter in the field to measure light conditions at the field site to allow for more accurate readings.

Examining sand lance foraging patterns across multiple tidal regimes and with different current speeds would also be valuable, as this area of research can be expanded upon (Witt 2011). Understanding sand lance foraging patterns would provide better insight into predator-prey interactions within the San Juan Channel ecosystem.

Finally, future studies could continue to monitor the San Juan Channel and Jackson Beach populations to determine if the cyclic pattern holds true across other years, and, if possible, to sample other sand wave fields in the San Juan archipelago for mature populations of sand lance.

Acknowledgements

I would like to extend a big thank you to the PEF advisors and TA—Matt Baker, W. Breck Tyler, Jan Newton, and Becca Guenther—who helped me navigate my project from start to finish; to my fellow PEF "scholars" and the Marine Biology students for their persistent optimism and assistance with fieldwork and GIS mapping (Jesse Kruttschnitt); to the *Centennial* crew—Dennis, Wolfe, Phil, and Craig—who made every cruise an adventure; and to my predecessors—Mary Rood, Alex Witt, Charlie Heller, and Thomas Pham—for providing me with such a wealth of information. Without you, this study would not have been possible.

References

Appenzeller AR, Leggett WC. 1995. An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). Canadian Journal of Fisheries and Aquatic Sciences. 52(3): 504-511.

Bailey KM, Canino MF, Napp JM, Spring SM, Brown AL. 1995. Contrasting years of prey levels, feeding conditions and mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. Marine Ecology Progress Series. 119(13):11-23.

Baker M. 2014. Personal communication.

Barton K. Cormorants and other seabirds in the San Juan Channel during fall 2014. Pelagic Ecosystem Functions Research Apprenticeship presentations. University of Washington, Friday Harbor Laboratories.

Blaine J. Pacific sand lance (*Ammodytes hexapterus*) present in the sand wave field of central San Juan Channel, WA: Abundance, density, maturity, and sediment association. Pelagic Ecosystem Functions Research Apprenticeship. University of Washington, Friday Harbor Laboratories.

Bollens SM, Frost BW, Schwaninger HR, Davis CS, Way KJ, Landsteiner MC. 1992. Seasonal plankton cycles in a temperate fjord and comments on the match mismatch hypothesis. Journal of Plankton Research. 14(9): 1279-1305.

Bynum K. 2014. Habitat use by Pacific sand lance in San Juan Channel, Fall 2014. Pelagic Ecosystem Functions Research Apprenticeship presentations. University of Washington, Friday Harbor Laboratories.

Clark CW and Levy DW. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist. 131(2): 271-290.

Cowx IG and Frear PA. 2004. Assessment of year class strength in freshwater recreational fish populations. Fisheries Management and Ecology. 11: 117-123.

Cougan C. 2014. Factors affecting San Juan Channel and Puget Sound water properties during fall. Pelagic Ecosystem Functions Research Apprenticeship presentations. University of Washington, Friday Harbor Laboratories.

Crecco VA, Savoy TF. 1984. Effects of fluctuations in hydrographic conditions on year class strength in American shad (*Alusa sapidissima*) in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences. 42:1640-1648.

Cushings DH, Horwood JW. 1994. The growth and death of fish larvae. Journal of Plankton Research. 16: 291-300.

Engelhard GH, van der Kooij J, Bell Ed, Pinnegar JK, Blanchard JL, Mackinson S, Righton DA. 2008. Fishing mortality versus natural predation on diurnally migrating sandeels *Ammodytes marinus*. Marine Ecology Progress Series. 369: 213-227.

Ewings L. Physical influences on spatial and temporal distribution of Pacific sand lance (*Ammodytes hexapterus*) in the sand wave fields of San Juan Channel. Biology 479 Class Papers. University of Washington, Friday Harbor Laboratories.

Fortier L, Ponton D, Gilbert M. 1995. The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. Marine Ecology Progress Series. 120:11-27.

Friedlaender AS, Hazen EL, Nowaxek DP, Halpin PN, Ware C, Weinrich MT, Hurst TP, Wiley D. 2009. Diel changes in humpback whale *Megaptera novaeangliae* feedingbehavior in response to sand lance *Ammodytes spp.* Behavior and distribution. Marine Ecology Progress Series. 395: 91-100.

Geiger AC. 1987. Trophic interactions and diurnal activity patterns of the Pacific sand lance, *Ammodytes hexapterus*, in the San Juan Channel, WA. Marine Fish Biology Class Papers. University of Washington, Friday Harbor Laboratories.

Greene GH, Wyllie-Echeverria T, Gunderson D, Bizarro J, Barrie V, Fresh K, Robinson C, Cacchione D, Pentilla D, Hampton M, Summers A. 2011. Deepwater Pacific sand lance (*Ammodytes hexapterus*) habitat evaluation and prediction in the Northwest Straights Region. Final Report, Northwest Straights Commission.

Haldorsen L, Paul AJ, Sterritt D, Watts J. 1989. Annual and seasonal variation in growth of larval walleye pollock and flathead sole in a southeastern Alaskan bay. Rapp PV Reun Cons Int Explor Mer. 191: 220-225.

Haldorsen L, Pritchett M, Sterritt D, Watts J. 1993. Abundance patterns of marine fish larvae during spring in a southeastern Alaskan Bay. Fishery Bulletin. US. 91: 36 44.

Hayes K. 2014. Abundance and distribution of harbor porpoises and other cetaceans in the SanJuan Channel: tides and bathymetry. Pelagic Ecosystem Functions Research Apprenticeship presentations. University of Washington, Friday Harbor Laboratories.

Heller CP. 2012. Distribution and variation between populations of Pacific sand lance in the San Juan Archipelago. Pelagic Ecosystem Functions Research Apprenticeship. University of Washington, Friday Harbor Laboratories.

Johnson SW, Thedinga JF, Monk KM. 2008. Distribution and use of shallow-water habitats by Pacific sand lances in southeastern Alaska. Transactions of the American Fisheries Society. 137(5).

Melnikov VN, Grudov KP, Bituma A. 1981. Analysis of diurnal vertical migrations of fish. Canadian translation of Fisheries and Aquatic Sciences. 4:108-112.

Mills CA and Mann RHK. 1985. Environmentally-induced fluctuations in year class strength and their implications for management. Journal of Fish Biology. 27(Suppl. A): 209-226.

Northwest Association of Networked Ocean Observing Systems (NANOOS). Data explorer. http://nvs.nanoos.org/Explorer

Pentcheff D. WWW Tide/Current Predictor. Biological Sciences, University of South Carolina. http://tbone.biol.sc.edu/tide/

Pham T. 2013. Spatiotemporal dynamics of Pacific sand lance (*Ammodytes hexapterus*) populations in the San Juan Archipelago during fall season. Pelagic Ecosystem Functions Research Apprenticeship. University of Washington, Friday Harbor Laboratories.

Robards MD, Wilson MF, Armstrong RH, Piatt JF. 1999. Sand lance: a review of biology and predator relations and annotated bibliography. USDA Forest Service Pacific Northwest Research Station Research Paper.

Rood M. 2010. Length distribution, condition factor, and feeding ecology of the Pacific sand lance in the San Juan Archipelago. Pelagic Ecosystem Functions Research Apprenticeship. University of Washington, Friday Harbor Laboratories.

Selbie DT. 2008. Large-scale exogenous forcing of long-term Pacific salmon production and ecosystem interactions in western North America. Queen's University (Canada) PhD Thesis.

Sisson N. 2012. Feeding ecology of the Pacific sand lance (*Ammodytes hexapterus*): Understanding the trophic role of an important forage fish in the San Juan Archipelago. Pelagic Ecosystem Functions Research Apprenticeship. University of Washington, Friday Harbor Laboratories.

Washington State Department of Ecology. Sand lance spawning beaches. Puget Sound Shorelines. http://www.ecy.wa.gov/programs/sea/pugetsound/species/sandlance.html

Witt A. 2011. Physical factors affecting the abundance and distribution of the Pacific sand lance *Ammodytes hexapterus* in the San Juan Archipelago. Biology 479 Class Papers. University of Washington, Friday Harbor Laboratories.

Wyllie-Echeverria T. 2010. Unpublished data.

Figures

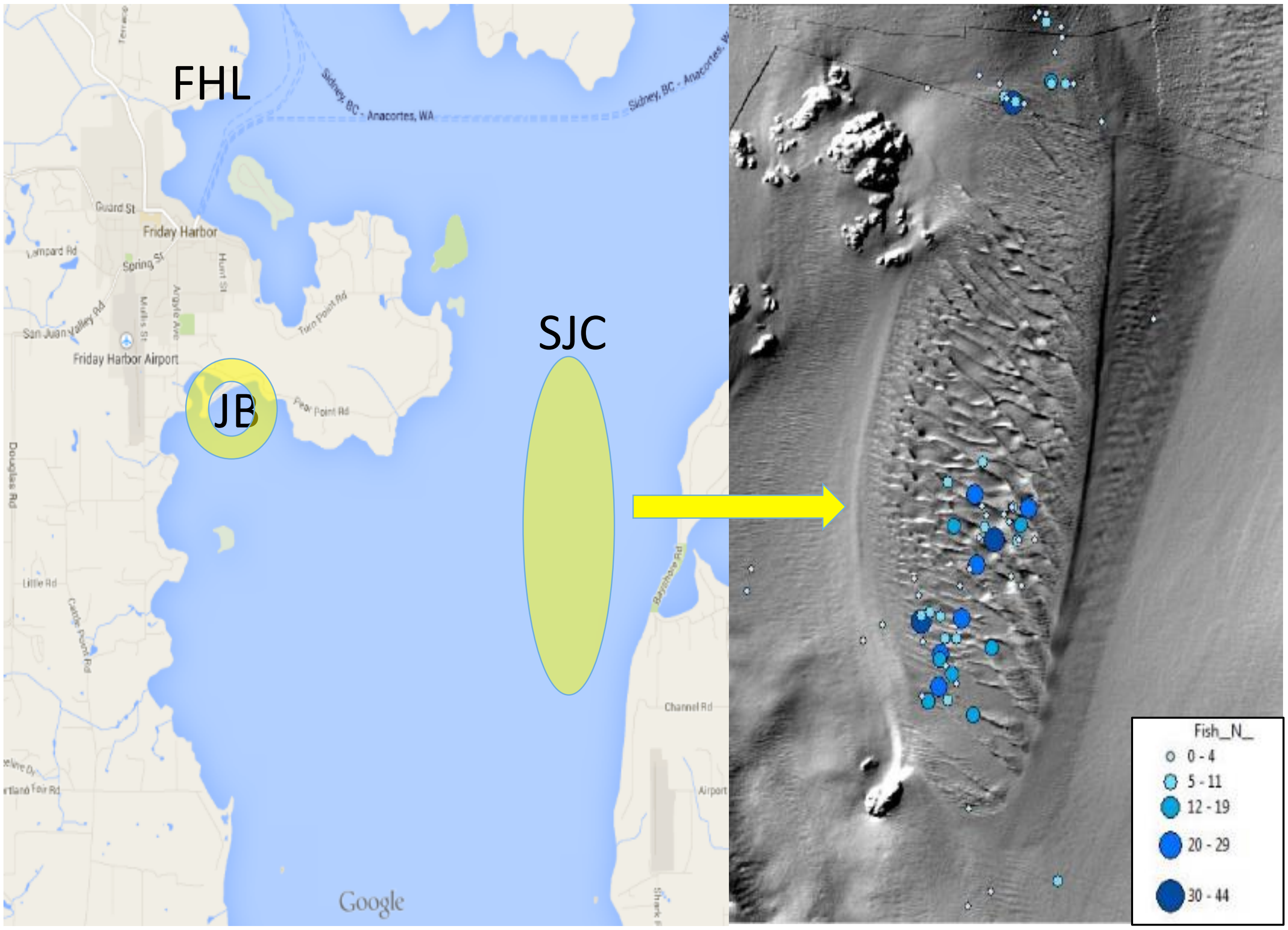

Figure 1. Van Veen sample areas in the San Juan Channel sand wave field (n=86 total grabs). Circle sizes and colors correspond to catch size; smaller, lighter circles had smaller catches and larger, darker circles had bigger catches.

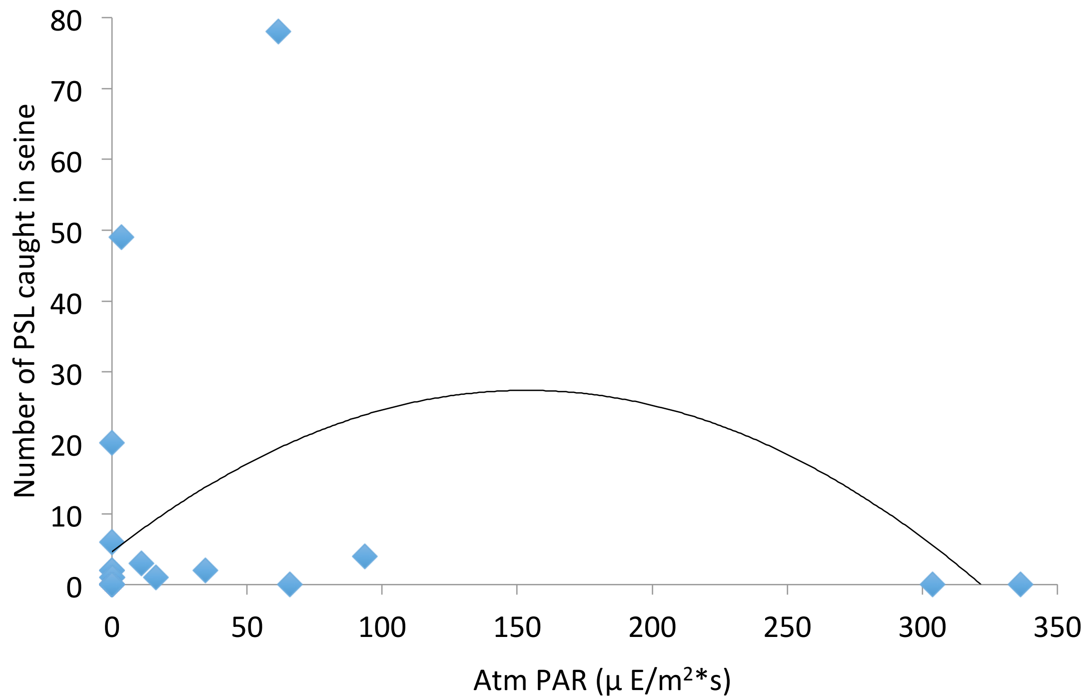

Figure 2. The pattern between atmospheric light (µE/m^2*s) and the number of sand lance caught in a seine at Jackson Beach (n=24 seines; R^2=0.1101, p=0.2939).

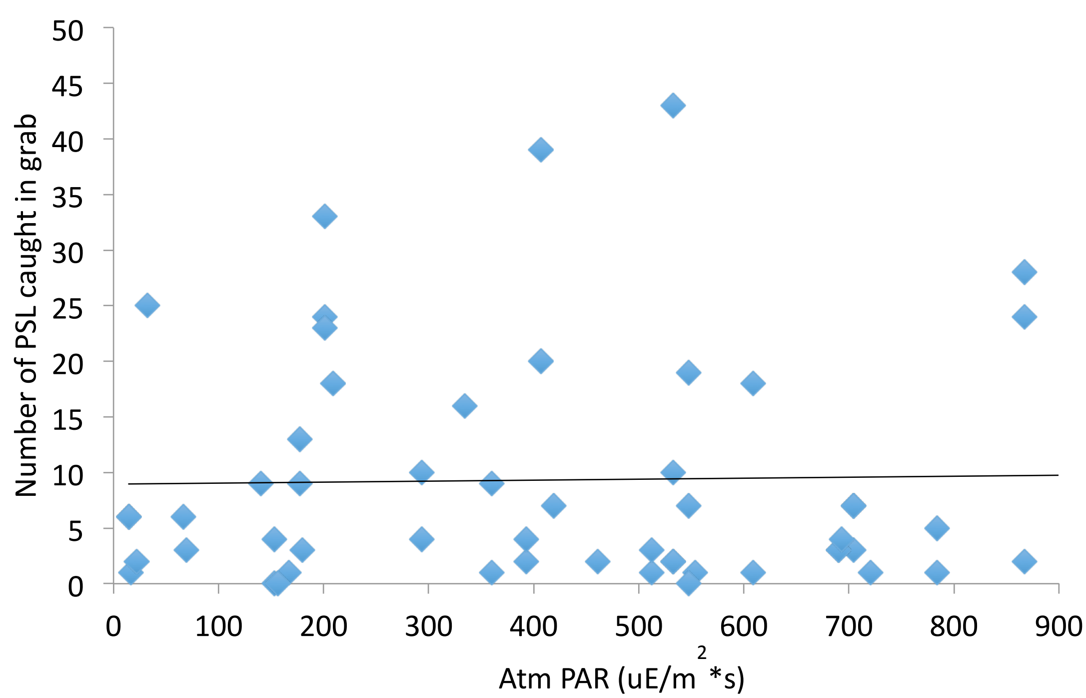

Figure 3. The number of sand lance caught in a Van Veen grab in the San Juan Channel at various levels of atmospheric light (µE/m^2*s) (n=62 grabs; R^2=0.0001, p=0.9977).

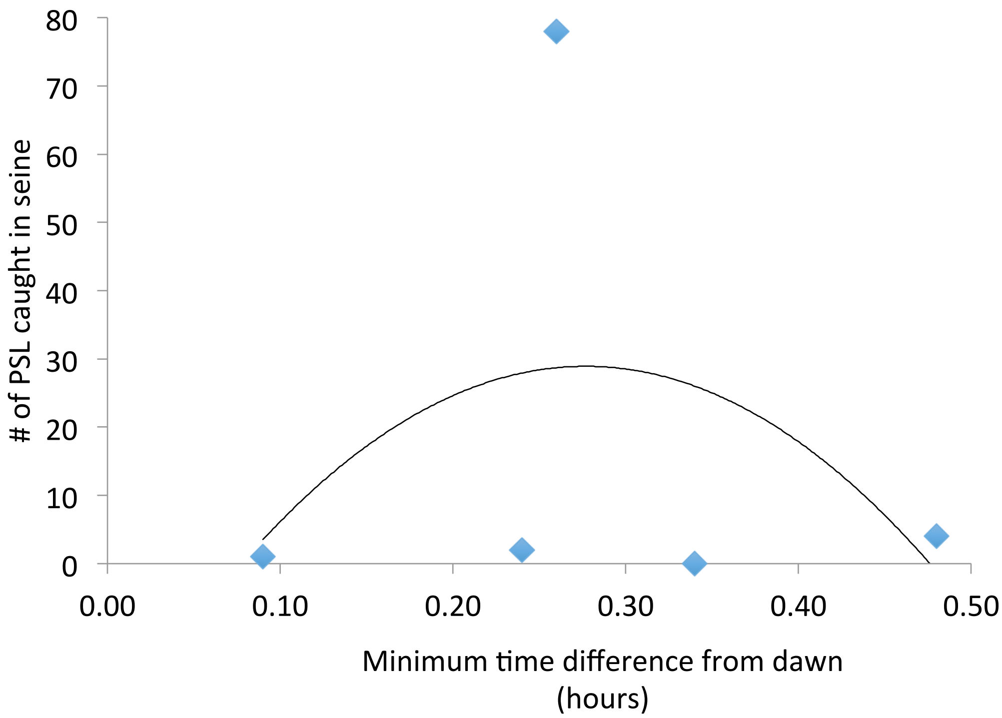

Figure 4. The number of PSL caught at Jackson Beach at dawn with respect to the minimum time difference from dawn (n=5 seines).

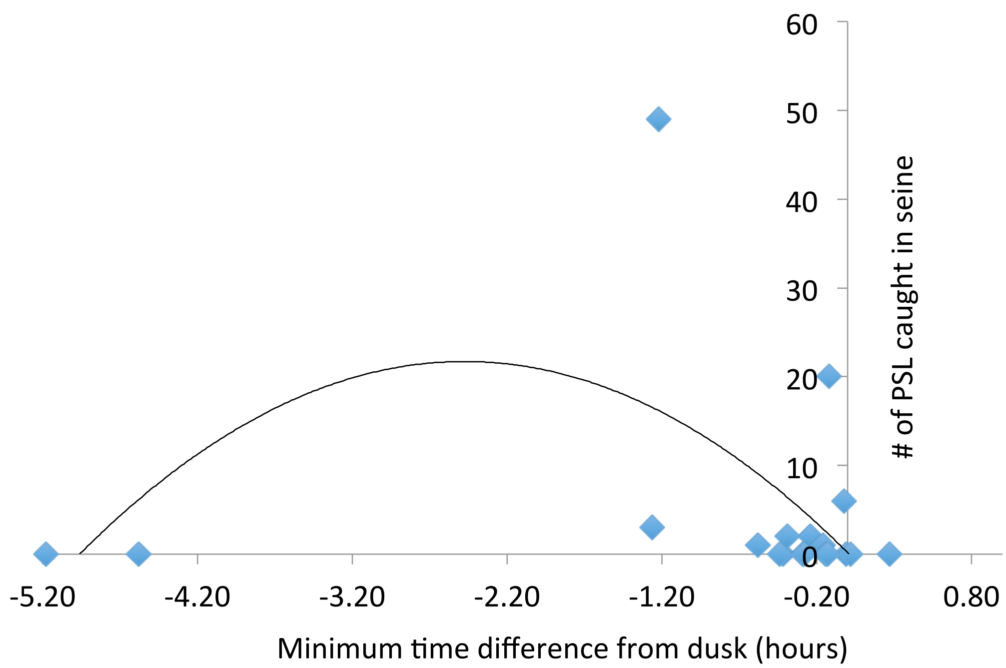

Figure 5. The number of PSL caught at Jackson Beach at dusk with respect to the minimum time difference from dusk (n=19 seines).

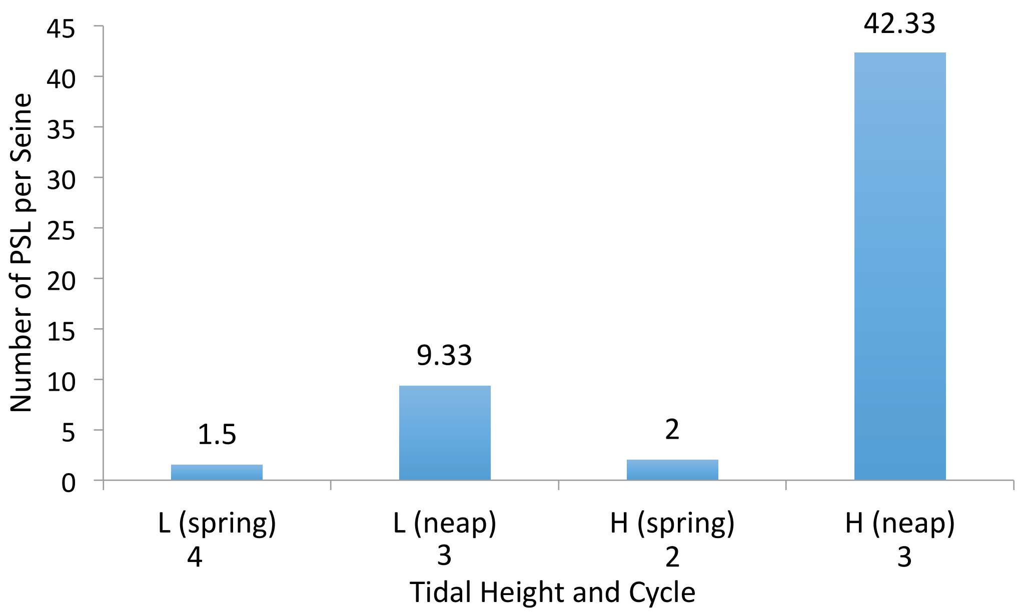

Figure 6. The number of sand lance caught at each tidal height and cycle at Jackson Beach (n=12 seines). Numbers above each bar are the average numbers of sand lance caught and numbers below each column are the number of seines performed during each sampling regiment.

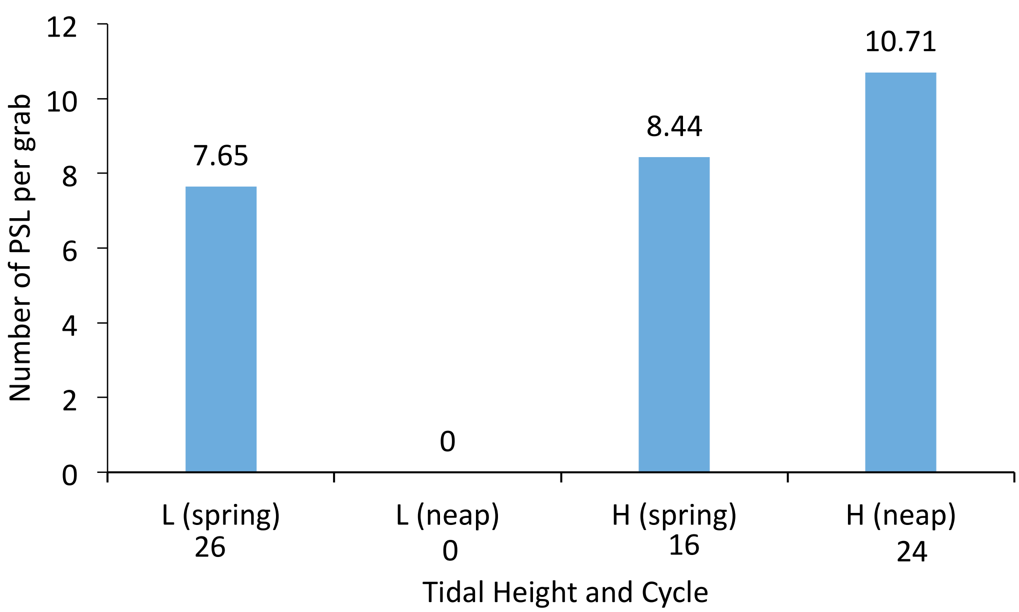

Figure 7. The number of sand lance caught at each tidal height and cycle in the San Juan Channel (n=66 grabs). Numbers above each bar are the average numbers of sand lance caught and numbers below each column are the number of grabs performed during each sampling regiment.

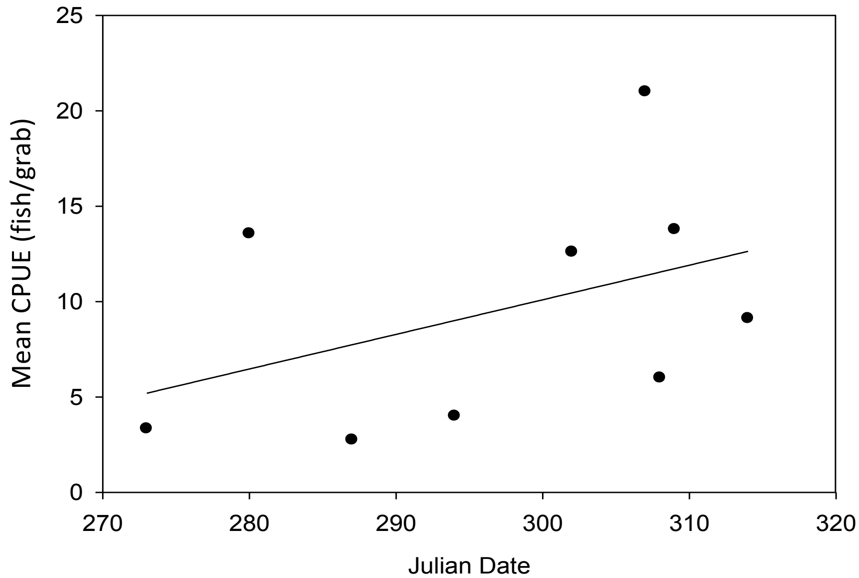

Figure 8. The San Juan Channel mean catch per unit effort (CPUE) across the fall 2014 season by sampling (Julian) date (n=9 days); R^2=0.1785, p=0.2558.

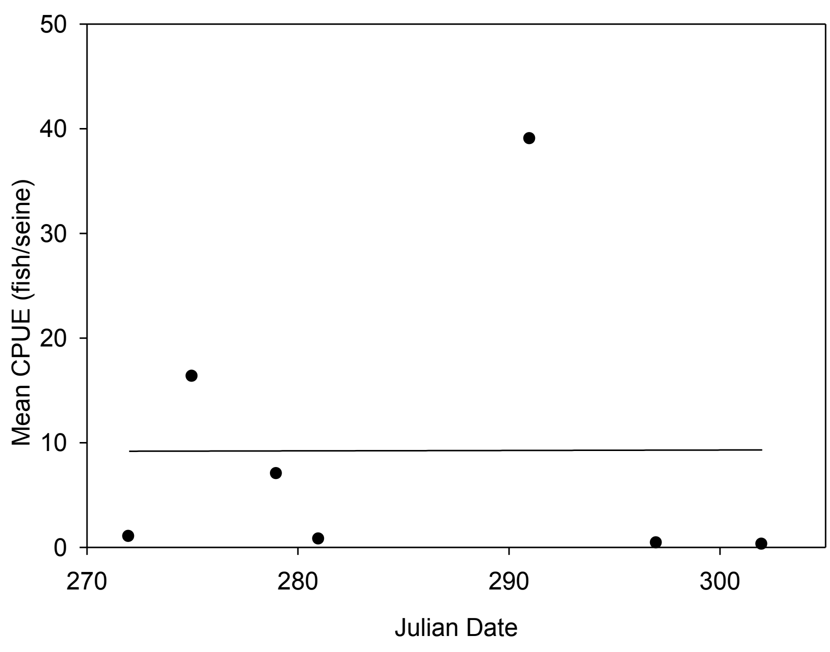

Figure 9. The Jackson Beach mean catch per unit effort (CPUE) across the fall 2014 season by sampling (Julian) date (n=7 days); $R^2=1.09*10^{-5}$, p=0.9944.

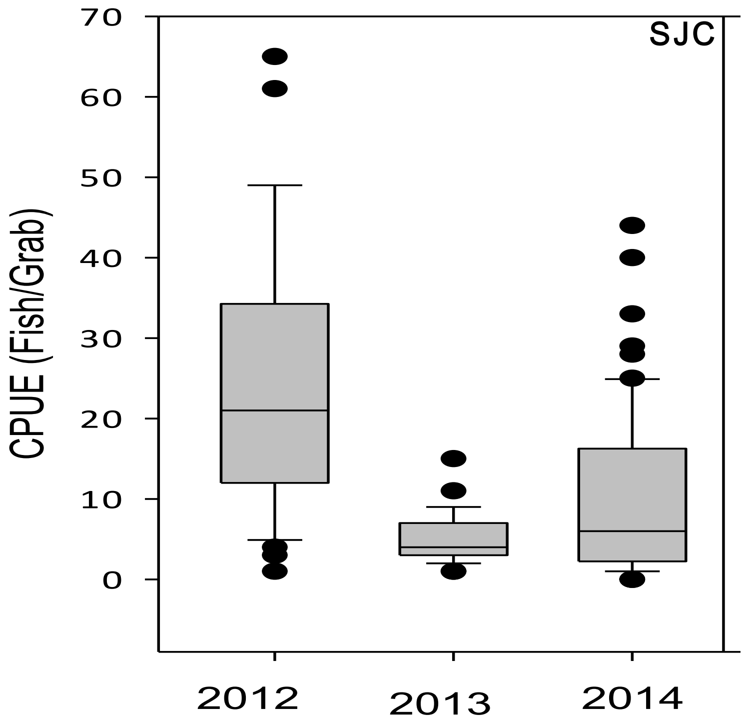

Figure 10. Inter-annual catch per unit effort (CPUE) in the San Juan Channel (SJC) from 2012-2014; mean ± SD: 24 ±17, 5 ± 3, 10 ± 10.

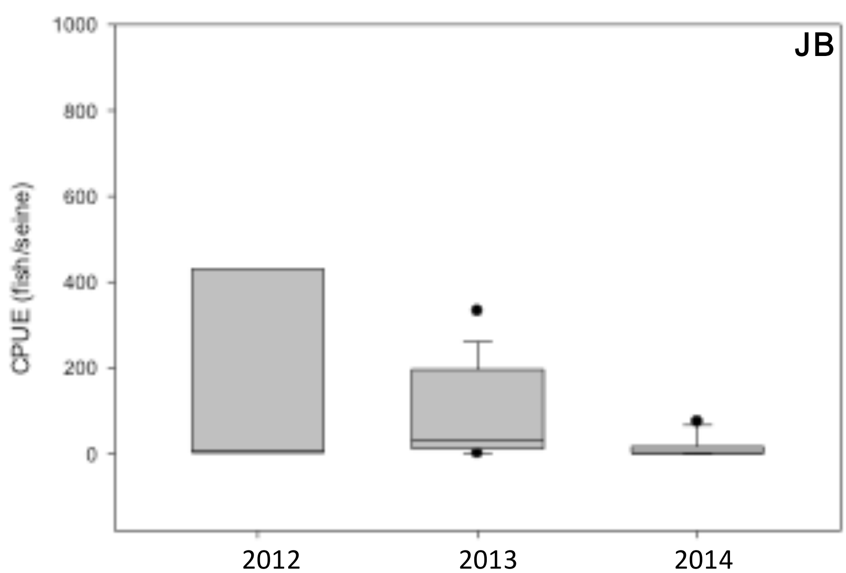

Figure 11. Inter-annual catch per unit effort (CPUE) at Jackson Beach (JB) from 2012-2014; mean ± SD: 174± 377; 85 ± 106; 14 ± 24.

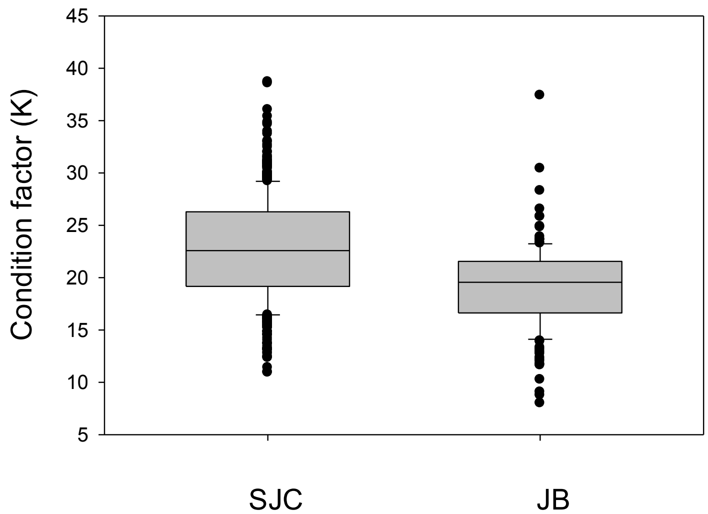

Figure 12. The condition factors (K) of sand lance from the San Juan Channel (SJC) and Jackson Beach (JB) from the fall 2014 season (n=586 and 165); mean ± SD: 22.8 ± 4.87, 19.01 ± 4.01.

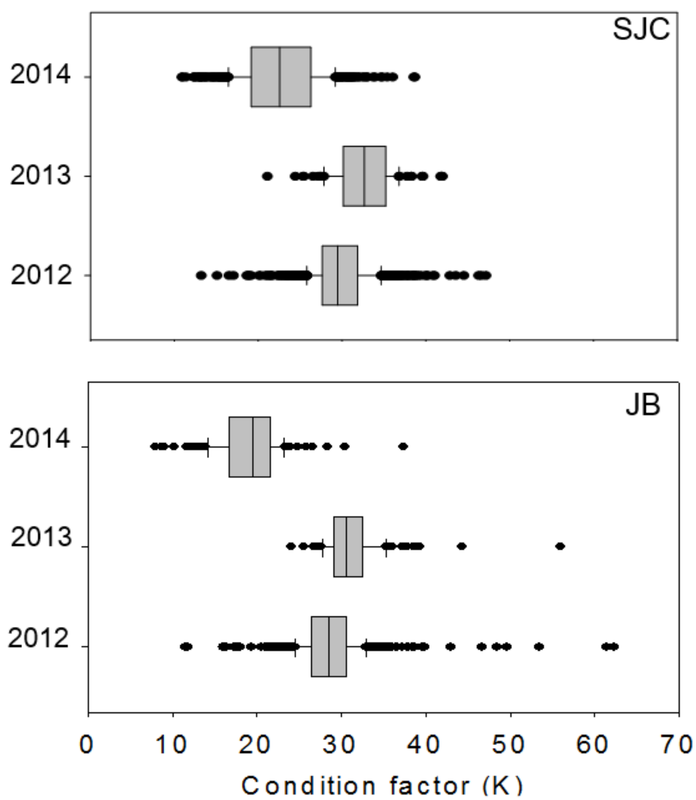

Figure 13. Fall condition factors (K) for sand lance in the San Juan Channel (SJC) and at Jackson Beach (JB) from 2012-2014.

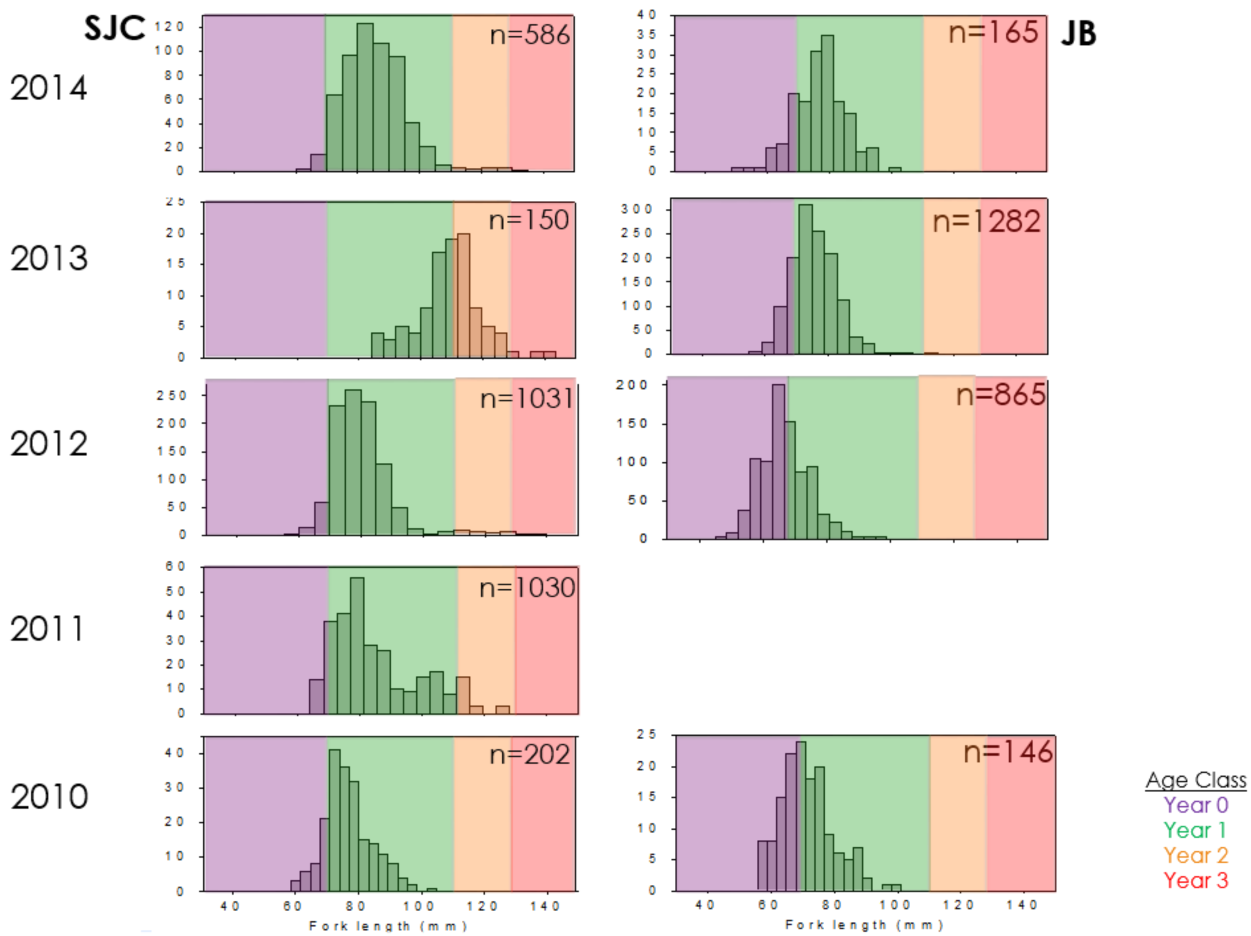

Figure 14. The distribution of fork lengths (mm) and age group structures for sand lance collected in the San Juan Channel (left column) and at Jackson Beach (right column). Colored bars represent age group classes and are based on fork lengths. Data was not available for Jackson Beach sand lance in 2011.

Figure 15. The fork lengths (mm) and corresponding age group classes for sand lance caught in the San Juan Channel (SJC) and at Jackson Beach (JB) from 2010-2014. Age classes: Year 0 (purple), Year 1 (green), Year 2 (orange), Year 3 (red).