Spatiotemporal Dynamics of Pacific Sand Lance (*Ammodytes hexapterus*) Populations in the San Juan Archipelago during Fall Season

Thomas Pham
University of Washington
Pelagic Ecosystem Function

Abstract

The Pacific sand lance (*Ammodytes hexapterus*) is an ecologically important forage fish in the Salish Sea serving as a link between secondary consumers and top predators. In this study we investigated variation in length, stomach fullness, condition factor, and catch per unit effort (CPUE) through the fall season in 2013 in order to infer the timing of overwintering dormancy. We also tested for differences between locations. Population structure and variation through the fall season were compared between populations at the San Juan Channel wave field and Jackson Beach and between past year’s findings (2006, 2010, 2012). The wave field population was significantly larger and was in greater condition than the population at Jackson Beach. Through the fall season for the wave field population: length remained stable, stomach fullness remained stable, condition factor declined, and CPUE remained stable. For the Jackson Beach population: length remained stable, stomach fullness declined, condition factor remained stable, and CPUE decline. These results suggest an earlier shift into overwintering dormancy for the wave field population compared to Jackson Beach.

Introduction

Fishes in the northern temperate zone are faced with strong seasonal variation in climate throughout the year. Temperature can vary drastically from summer to winter. Winter therefore can serve as a period of high mortality for fishes due to thermal stress, starvation, predation, or parasites and pathogens (Hurst, 2007). Poor winter conditions can disrupt populations in two different ways. Anomalously low winters temperatures have been observed to wipe out large numbers of fish, in what is referred to as winterkills. Winterkills can wipe out stocks indiscriminately but winter conditions can select against certain age classes. Studies on metabolic allometry have established that proportionally higher rates of consumption, growth, and energy depletion are observed in smaller fish (Post and Parkinson, 2001; Shuter and Post, 1990). This relationship has been observed across taxa. Consequently, smaller fish tend to consume energy more quickly, are not as efficient in building up energy reserves, and use them up more quickly. As such, small fish are more vulnerable to the effects of starvation and thermal stress (Hurst, 2007).
The Pacific sand lance (Ammodytes hexapterus) is a small forage fish commonly found in the North Eastern Pacific ranging from California to the Beaufort Sea and as westerly as the Sea of Okhotsk (Craig, 1984; Hashimoto, 1984; Robards et al., 1999b). A. hexapterus is one of six recognized species of sand lance and is the only one present in the northeastern Pacific (Fields, 1988). Pacific sand lance (PSL) is of great ecological importance within the Salish Sea acting as a primary link between secondary producers and top predators. They primarily feed on calanoid copepods and are responsible for transferring energy from zooplankton to many predators including a host of seabirds, fishes, and marine mammals (Fields, 1988; Robards et al., 1999b). Evidence throughout the literature recognizes a positive correlation between PSL abundance and seabird reproductive success (Robards et al., 1999b).

In regions of seasonal fluctuations, selection has favored life cycle adaptations that reduce the cost of winter mortality and maximizes fitness. During the winter, foragers such as PSL are faced with a trade-off between energy maximization and predator avoidance. At some point late through the year, the cost of foraging becomes too high as the availability of prey decreases. Therefore the strategy adopted is to build up energy reserves earlier in the season and overwinter in a state of dormancy characterized by limited feeding behavior, and reduced metabolism (Schultz and Conover, 1999; van Deurs et al., 2010). In this way, populations are able to minimize losses due to predation and starvation, which can be exacerbated by limited food availability. As they begin to overwinter, they shift from active foraging to burying themselves in the sediment as they become dependent on their energy reserves.

The main objective of this study was to characterize PSL population structure in terms of age, stomach fullness, condition factor, and catch per unit effort (CPUE) at the San Juan Channel wave field and Jackson Beach for the autumn season in 2013. By tracking variation throughout the season we hoped to identify the timing of passive overwintering behavior. And finally we compared population structure and pattern variations through the fall season across multiple years (Rood, 2010; Heller, 2012; Sisson, 2012) to determine if similar patterns were persistent on an inter-annual scale.

Methods

Study Site

Two different sites were used for our study. Along the San Juan Channel we traversed a 21.5km long transect. Beginning at the North station, adjacent to Yellow Island, (48°35.00’ N, 123°02.50’ W) we traveled to South station (48°25.20’ N, 122°56.60’ W), which is located west of the southern-most point of Lopez Island and south of Cattle Pass, the mouth of the San Juan Channel. Within the channel PSL sampling was specifically targeted at a known sand wave field located in the middle of the channel between San Juan Island and Lopez Island between 48°31.333‘-48°30.333’ N and 122°57.083‘-122°57.167’ W. Our motivation for using this particular sand wave field was driven by successful capture of PSL in prior studies (Blaine, 2006;
Van Veen Sediment Grabs

Along the San Juan Channel transect and within the range of the sand wave field, samples were collected aboard the R/V Centennial on six cruises from 9/13/2013 – 11/5/2013. Sampling was collected using a Van Veen Grab Sampler, a clamshell bucket which when dropped to the bottom of the ocean grabs approximately 0.12m$^2$ of sediment. Five drops were done between 1300 and 1500 on each cruise with the exception of 10/22/2013 and 11/5/2013 in which 7 and 11 drops were made respectively. A total of 38 grabs were done throughout the study. Each sample was placed in a large plastic tub releasing all the contents of the grab. The sediment was sifted through and filtered for fish. Captured fish were placed in a plastic bottle filled with seawater and euthanized using tricaine methanesulfonate (MS-222) and preserved using at least 30mL of buffered formalin. Coordinates, time, tidal phase, and number of fish collected were recorded for each grab.

Seine Net

Beach seines were performed 1-2 times a week beginning on 9/30/2013 – 11/15/2013 at Jackson Beach. Weather and time permitting seines were taken at both dawn and dusk. Dawn and dusk were chosen as our sampling period given the crepuscular behavior of PSL. They will bury themselves in benthic substrate during the day and switch to schooling and foraging at dawn and dusk (Hobson, 1986; Inoue et al. 1967). The small motorboats Coot and Auklet were used to transport and perform the seines. The net used was made of knotless nylon mesh measuring 36.6m long and 3.7m deep. Ropes were tied to each end of the net. One side of the net was kept about 1m from shore. The motorboat was driven in an arc from the starting point while another person deployed the net off the bow slowly. The other end of the net was handed off to a second person on the shore and then both ropes were simultaneously pulled onto the shore. The net was then filtered for sand lance and euthanized and preserved in the same manner as on the cruises. Non-target organisms were released.

Length, Mass, Condition Factor, and Age

Morphometrics were recorded in the lab for each individual. Measurements for fork length and total length were taken using a standard ruler. Mass was measured to the nearest 0.001 gram using a Mettler Toledo digital scale. Condition of PSL was calculated using a modified Fulton condition factor ($K$) proposed by Bagenal and Tesch (1978).

$$K = \frac{M}{L^3} \times 10^{7.3}$$  

Equation 1.

Where $M$ = mass (g) and $L$ = length (mm). $K$ = condition factor.
Age estimation was based on findings by Greene and Echeverria (unpublished data). Fish were assumed to be young of the year if less than 70mm, one year old if between 70-109mm, two years old if between 110-129mm, and three years old if between 130-150mm.

**Stomach Analysis**

Stomachs of fish were dissected and examined to determine stomach fullness. All available fish caught in the sand wave field were examined (n = 109, total = 150), but only a subsample at Jackson Beach was examined (n = 409, total = 1589) due to time restraints. It must be noted that a different metric for stomach fullness was used in 2012. Stomach fullness was assessed qualitatively using a rank system (0 – empty to 4 – full), while a quantitative method was used for this study. On the ventral side of the fish, an excision was made from below the mouth posteriorly towards the anus using a scalpel. Stomachs were then removed using forceps and placed onto a petri dish. Stomachs were weighed with and without contents. An index was created to quantify stomach fullness.

\[
R = \frac{S - S_0}{S_0}
\]

Where \( S = \) stomach mass (g) including contents and \( S_0 = \) stomach mass (g) excluding contents. \( R = \) Stomach fullness ratio.

**Results**

**Comparison of San Juan Channel and Jackson Beach 2013**

**Population Structure (length, stomach fullness, condition factor)**

A total of 1739 individuals were collected and measured for fork length, total length, and weight. Sampling at the sand wave field took place between 9/13/2013 - 11/5/2013 and a total of 150 individuals were collected. Sampling at Jackson Beach occurred between 9/30/2013 – 11/15/2013 and a total of 1589 total individuals were collected.

Significant differences between populations were found for mean fork length, stomach fullness, and condition factor. Fork length ranged from 79-143.5 mm with a mean of 108 mm (± 0.85 SE) for the population present at the sand wave field, while at Jackson Beach fork length ranged from 53-115 mm with a mean of 75 mm (± 0.18 SE) (Fig. 2). Stomach fullness ratio ranged from 1.00-1.96 with a mean of 1.07 (± 0.01 SE) (Fig. 3) for the sand wave field population, while at Jackson Beach the stomach fullness ratio ranged from 1.00-9.40 with a mean of 1.67 (± 0.06 SE). Condition factor ranged from 21.09 – 41.98 with a mean of 32.02 (± 0.29 SE) (Fig. 4) for the sand wave field population, while at Jackson Beach the stomach fullness ratio ranged from 12.55 – 53.19 with a mean of 30.02 (± 0.08 SE).
Within season variation (length, stomach fullness, condition factor, CPUE)

Variation through the fall season was tracked at both the sand wave field and Jackson Beach for length, stomach fullness, condition factor, and CPUE. Variation in fork length remained stable and no apparent trend was observed at either the San Juan Channel or Jackson Beach (Fig. 5). The remaining three factors were examined in order to make assumptions regarding overwintering behavior. Stomach fullness ratio declined through season and both populations (Fig. 6). A slight yet significant decline in stomach fullness ratio was observed at the sand wave field population through the season, while an even steeper decline was observed for the Jackson Beach population.

Variation in condition factor through the season differed between populations. A significant decline was observed at the sand wave field, although with a weak relationship (Fig. 7). In contrast no net change in condition factor was observed over time at Jackson Beach.

Within the sand wave field, a total of 150 fish were collected from 38 Van Veen grabs and at Jackson Beach a total of 1589 fish were collected from 32 seines. No net change was apparent for CPUE at the sand wave field over time (Fig. 8). At Jackson Beach a decline over time was observed but variance was high and the relationship was insignificant.

Inter-annual variation

Population structure (Length, catch per unit effort)

Data was used from previous studies to compare and contrast this year’s findings with that of 2010 (Rood, 2010) and 2012 (Heller, 2012; Sisson, 2012). Sampling from these years was also within the San Juan Channel sand wave field. There were some differences between sampling timing and frequency, but overall it was similar enough for cross comparison. Findings from 2010 were only compared in terms of length distribution. Age class structure was assumed under the age at length relationship (Greene and Wyllie-Echeverria, unpublished data).

2010 and 2012 had very similar age class structure comprising mostly of 1 year olds (70-109 mm) and some young of the year (YOY) (0-69 mm). The only difference was the presence of a small number of 2 year olds (110-129 mm) in 2012. In contrast, 2013 had a starkly different age class structure. 2013 was comprised of almost evenly split 1 and 2 year olds with no YOY present at all.

Despite similar sampling effort (2012 – 43 grabs, 2013 – 38 grabs), sediment collected, and sampling period there were stark differences in catch between 2012 and 2013. An order of magnitude fewer fish this were collected this year (n = 150) compared to last year (n = 1031).

Within season variation (stomach fullness, condition factor, CPUE)

Findings from 2012 (Heller, 2012; Sisson, 2012) were also compared against our finds this year in terms of seasonal variation to confirm patterns for stomach fullness, condition factor and CPUE for populations at the sand wave field. Stomach fullness declined through the season in 2012 while a minor yet significant decline was observed in 2013. No apparent trend
was observed for condition factor over the season in 2012, while a slight yet significant decline in condition factor was observed through the season in 2013. An increasing trend in CPUE was observed through the season in 2012. In contrast no trend was observed through the season for 2013, as CPUE remained stable.

**Discussion**

Characterizing population structure can allow baseline data to be established and offer insight in shifts in population dynamics over time. Here we present the characterization of *A. hexapterus* populations during the fall season of 2013. Significant differences were observed between the San Juan Channel sand wave field and the Jackson Beach populations. Length frequency distribution differed greatly (Fig. 1). Given age at length relationships (Greene and Wyllie-Echeverria, unpublished data) we can presume a much younger population at Jackson Beach compared to the sand wave field. The differences in mean fork length indicate an age discrepancy of nearly a full year between locations. These findings are consistent with previous studies that the sand wave field population is longer and older (Rood, 2010, Heller, 2012), although the differences between mean population lengths were much greater than previously observed. Jackson Beach is known spawning habitat for PSL and therefore would be expected to contain a large amount of YOY and 1 year old fish.

Stomach fullness and condition factor were assessed between both sites indicating differences in feeding. It is important to note that we were limited in our ability to sample consistently at both locations. A Van Veen grab was used at the sand wave field and a seine net was used at Jackson Beach. Despite differences in capture we believe they are nonetheless comparable. Inoue et al. (1967) found normal gut evacuation time for *A. personatus* to be about 12 hours while Ciannelli (1997) found PSL to have a prolonged gut evacuation time of 45-80 hours during the winter and the ability to retain food in their stomachs for up to 30 hours. We therefore would expect individuals to retain food in their stomachs regardless of what time of day sampling occurred. Mean stomach fullness ratio at the sand wave field suggests that the population had ceased to feed while the ratio at Jackson Beach suggests that they were still feeding later into the season (Fig. 3). Condition factor can be used to examine general energy storage within fish and has been used as a metric to examine somatic energy content in PSL (Robards et al., 1999a). Differences in mean condition factor between the sand wave field and Jackson beach were minimal although significantly different (Fig.4). These findings are consistent with what we would expect to observe, given that smaller fish tend to build up energy reserves less efficiently than larger fish (Post and Parkinson, 2001; Shuter and Post, 1990). These differences between populations suggest that the larger (older) population is better prepared to overwinter than the population at Jackson beach.

CPUE is a common metric used in fisheries as an indirect measure of abundance. Due to the nature of our differing methodology between the sand wave field and Jackson Beach, differences in CPUE were not comparable. Sampling in the sand wave field captured fish inactive fish buried in the sediment, while sampling at Jackson Beach captured fish actively
foraging in the water column. Further investigation on differences in abundance between locations may be accomplished by standardizing the sampling method. We suggest using a Van Veen grab to directly sample in the substrate right along the shore of Jackson Beach, as sampling in the water column at the wave field will likely have a great deal of patchiness.

Mean fork length was examined over time throughout the season at both sites. A large shift in fork length over a short period of time might suggest migration of age classes, although size selective mortality could also be a possibility. This could also be suggestive of older fish migrating to the intertidal zone for reproduction. Further study at Jackson Beach could be expanded to determine timing of reproduction. PSL typically spawn between late September and October on sandy beaches (Robards 1999). It may be difficult to detect eggs as they blend in with the sand. However, spawning events for PSL are believed to be dominated by males in a 2:1 ratio. Sex ratio determination at Jackson Beach and continued observation for eggs during dissections could offer understanding into the timing of spawning events.

Overwintering serves as a prime strategy for planktivorous fish that face strong seasonal fluctuations in prey availability, day length, and temperature (van Deurs et al., 2010). In the present study we tracked variations in stomach fullness, condition factor, and CPUE for overwintering behavior. Within the sand wave field there was a very slight decline in stomach fullness over the course of the season (Fig. 6). CPUE remained stable throughout the season and condition factor declined moderately (Fig. 7) (Fig. 8). The most significant trend here is that condition factor declined over time, indicating that the population has ceased feeding and has begun to depend on their energy reserves. The majority of the stomachs examine were empty (stomach fullness ratio < 1.05, 69.7%) which also supports our belief that this population has already begun passive behavior. These trends together suggest that we missed the transition into dormancy, and that the population has already begun to overwinter.

Within Jackson Beach there was a steep decline in stomach fullness over the course of the season but condition factor stayed relatively the same (Fig.6) (Fig. 7). This suggests that the Jackson Beach population was feeding later into the season because stomach fullness is declining but they have not yet begun to depend on their reserves, as indicated by the stable condition factor. There was a decline in CPUE although the relationship was statistically insignificant (Fig. 8). Still, this trend is consistent with what we would expect as less fish should tend to forage in the water column later in the season as they begin to overwinter. Here we indicate that the Jackson Beach population is transitioning into overwintering dormancy.

Our study continues upon a series of studies examining PSL within the sand wave field. Previous studies have been able to identify the timing of the shift into overwintering dormancy (Rood, 2010; Heller, 2012; Sisson, 2012). Although there can year to year variability, it is interesting to note that our results suggest an earlier shift than in 2010 and 2012. Length frequency distribution was compared across four years (2006, 2010, 2012, and 2013) of PSL studies at Friday Harbor Laboratories (Blaine, 2006; Rood, 2010; Heller, 2012; Sisson, 2012). 2013 was quite anomalous compared to previous age-class structures. 2006, 2010, and 2012 were dominated by 1 year olds. 2006 and 2010 had a limited number of YOY, and 2012 had small amount of both YOY and 2 year olds. In contrast, no YOY were present at all in 2013. 2013
was characterized by a near 50:50 split of 1 and 2 year olds. The lack of YOY is particularly interesting because they were observed in previous years. Size selective mortality could be one explanation. The match/mismatch hypothesis proposes that variations in year class strength are due to the rigid nature of spawning time and the variability of phytoplankton blooms (Cushing, 1990). The larval stage is critical for growth and development and is a period of high vulnerability. If suitable food is neither abundant nor available, it can lead to mass mortality by means of gape limitation. This can be a function of not having a great enough gape to consume quality prey or by being too small and thus fitting the gape of a greater number of predators. The lack of YOY present in the age class structure for 2013 may infer that the newly hatched fish missed the timing of abundant copepods earlier this spring or that perhaps secondary production was too low to support that cohort. Fortier (1995) found PSL populations to follow the match/mismatch hypothesis at Hudson Bay, Canada. Variability in feeding success and growth was dependent on the dynamics of cyclocoid copepods. Better understanding of the overwintering behavior of PSL is essential for understanding population dynamics presently and in the future.

Acknowledgements

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References


Table 1. Sampling effort at San Juan Channel

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<th># Fish Caught</th>
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Table 2. Sampling effort at Jackson Beach

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Figure 1. Fork length (mm) frequency of *A. hexapterus* at the San Juan Channel (n =150) and Jackson Beach (n= 1589)
Figure 2. Boxplot for fork length (mm) at the San Juan Channel (mean = 108.94mm) and Jackson Beach (mean = 75.20mm). ANOVA: F_{1,1737}=2848, P=0.000.
Figure 3. Boxplot for stomach fullness ratio (stomach with contents: stomach) at the San Juan Channel (mean = 1.07) and Jackson Beach (mean = 1.67). ANOVA: $F_{1,516}=31.98$, $P=0.000$. 
Figure 4. Boxplot for condition factor (K) at the San Juan Channel (mean = 32.02) and Jackson Beach (mean = 30.02). ANOVA: $F_{1,1737}=50.41$, $P=0.000$. 
Figure 5. Mean fork length (mm) of *A. hexapterus* at the San Juan Channel and Jackson Beach through the fall season. Error bars expressed as standard error.
Figure 6. Mean stomach fullness ratio of *A. hexapterus* at the San Juan Channel and Jackson Beach through the fall season. Error bars expressed as standard error.
Figure 7. Mean condition factor (K) of *A. hexapterus* at the San Juan Channel and Jackson Beach through the fall season. Error bars expressed as standard error.
Figure 8. Mean condition CPUE of *A. hexapterus* at the San Juan Channel and Jackson Beach through the fall season. Error bars expressed as standard error.