Diet and Feeding Behavior in *Ammodytes personatus* and Other Pelagic Fish

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Pelagic Ecosystem Function Research Apprenticeship

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Abstract:

Like many marine ecosystems, the San Juan Archipelago has several critical species of forage fish in the middle trophic level. These species play a critical role in energy transfer. This study examines variations in diet across different species, locations, and seasons. I studied the Pacific sand lance, Pacific herring, and Surf smelt. In contrast to past studies that indicated PSL were preferential to calanoid copepods, in my analyses PSL appeared to feed on a combination of amphipods and copepods, while herring and smelt fed primarily on copepods. In comparing sand lance across multiple sampling locations, both in an established nearshore population at Jackson Beach and a newly discovered nearshore population at South Beach, we noted feeding activity and foraging behavior. PSL at South Beach eat primarily copepods whereas PSL in Jackson Beach are eating both amphipods and copepods. In contrast, no observable feeding activity was measured in the larger, older fish in the offshore location that we measured on multiple occasions (San Juan Channel Wave Field). Upon examining San Juan Channel data from spring 2015, fish appeared to be leaving their winter dormancy period. Based on this new data, the winter dormancy period was estimated to be between late February and early October.

Introduction:

The San Juan Archipelago is home to a rich and diverse community of forage fish, which comprise a vital link in the marine food chain. According to the wasp waist model, these fish regulate the upper and lower trophic levels, specifically the flow of energy between these two levels (Cury *et al*. 2000). Because of their impact on other fish, birds, and marine mammals, it is important to understand their local feeding ecology. To understand how the transfer of energy, we need to look at diet.

In the Archipelago, there are three key forage fish species *Ammodytes personatus*, the Pacific sand lance, *Clupea palasii,* the Pacific herring, and *Hypomesus pretiosus,* the Surf smelt, all of which occupy a similar trophic niche. The PSL is known to be a planktivorous fish, feeding on mainly calanoid copepods (Rood 2010, Sisson 2012, Highland 2013, Burke 2014, Cieri 2015). The other forage fish share a similar diet, but have differing life strategies compared to the PSL.

One of the largest differences in lifestyles occurs during winter. Foraging is energetically expensive for PSL, as they do not possess a swim bladder. When productivity gets too low, PSL are known to enter a period of winter dormancy in the San Juan Channel Pacific Wave Field in order to conserve energy and to avoid predation (Robards 1999). Winter dormancy is defined as a period of inactivity occurring during the winter. During this time, dormant fish remain inactive, cease eating, and reduce protein synthesis and growth (Campbell 2008). Although this dormancy is an important part in the PSL life strategy, the exact timing of it is not yet understood.

I studied various aspects of the feeding ecology of PSL compared to different variables across the fall season. I compared PSL diet to the prey field available at Jackson Beach and between two other species of forage fish, Pacific herring and Surf smelt. I also studied trends in stomach fullness over the course of the fall season, and compared that data to past years.

Methods:

Prey Field Analysis:

A prey field sample was performed at Jackson Beach. 30 second horizontal plankton tows were performed on site with a 150μm net. Samples were fixed in formalin for later analyses. Samples were not split due to low plankton density. Samples were analyzed in a Bogorov Chamber. Taxa were counted individually and recorded.

Fish Collection:

Fish were collected from several different locations over the course of the season, including Jackson Beach (JB), San Juan Channel (SJC), South Beach (SoB), Salmon Bank (SaB), and Iceberg Point (IP) (Figure 1). Fish collected from Jackson Beach were caught using a combination of boat seining and walking seine. The fish collected from South Beach were only sampled using the walking seine. The van-veen grab was used on the R/V Centennial and R/V Auklet in offshore locations of SaB,IP,SJC,JB-sediments sampled from the Pacific Sand Wave in the San Juan Channel. All fish were euthanized using MS-222 (tricaine methanesulfonate), measured for length and weight, observed for coloration and stored in formalin, separated by cast number and location (on occasions where otoliths and genetics samples were retained, heads and tails removed prior to storage in formalin).

Fish Analysis:

Protocol for all sampled fish entailed measurement, examination of color of the dorsal side of fish, and a subset of fish were chosen for preservation and subsequent diet analyses. Upon removal from the preservative, length and weights were taken again for each fish. In order to collect stomachs, scissors were used to cut along the ventral side of the fish, starting at the anus and ending at the lower jaw (see Burke). All body cavity contents were removed and stored in 95% ethanol for later analysis.

Upon analysis, stomachs were separated from the other organs and the full stomach was weighed and recorded. Stomachs were cut in half, and contents were pushed out from both sides and examined under a dissecting microscope (see Sisson 2012). Contents were spread out with sterile water and counted over the entire petri dish. Individual taxa of plankton were counted and recorded. Anything that was too digested was labeled as unidentified. Empty stomach weights were recorded after all contents had been counted.

Stomach fullness ratio was calculated for each stomach sampled. This was done by dividing the weight of the full stomach by the weight of the empty stomach (Cieri, 2015). An empty stomach would equal a value of 1. If the scale read 0.00, the value was recorded as 0.01

Diet Analysis:

After removal from the stomachs, plankton were counted and recorded per identifiable taxa. To determine numerical percent composition, the prey percentages were determined for each individual fish, and then averaged across all fish (Ahlbeck, *et al.*, 2012). This was done for PSL, PH, and SS.

Results:

Analysis of prey field available to forage fish:

The prey field at Jackson Beach consisted of 13 different plankton taxa. Calanoid copepods were the dominant group, comprising 90% of the prey field (Figure 2). Amphipods composed a small amount of the prey field, making up 7% of the total prey field. The remaining taxa appeared very scarcely, but were still noted.

Analysis of forage fish diets:

During fall, diet varied noticeably among the three forage fish species. Pacific sand lance diet this year consisted primarily of two taxa of plankton, calanoid copepods and amphipods (Figure 3). Amphipods made up the largest proportion of the PSL diet, nearly 50%. Adult calanoid copepods comprised 36% of the Pacific sand lance diet, with the nauplii making up only 4% of the diet. Euphausiids also comprised 4% of the diet, and the remaining individuals were too digested to identify. Similarly, Pacific herring ate mainly adult calanoid copepods (Figure 4). The diet consisted of a higher proportion of adult calanoid copepods, 65% of the total diet. Amphipods made up only 16% of the diet. The rest of the stomach contents were too digested to identify. Surf smelt diet consisted almost entirely of calanoid copepods, 88% (Figure 5). Amphipods composed a small portion of the total diet, while the remaining proportion was too digested to identify.

Spatial Variation:

The Pacific sand lance at South Beach diet consisted of mainly copepods, comprising 75% of the diet, while copepod nauplius composed 21% (Figure 6). The remaining 4% consisted of other taxa that appeared very few times and are categorized as “other.” Fish sampled at San

Juan Channel, Salmon Bank, and Iceberg Point were empty, and diet analyses were not performed.

Stomach Fullness:

Fish from San Juan Channel had empty stomachs for the course of the fall transition (Figure 7). On the first date, one fish had contents in its stomach, but this is considered an outlier. However, for the rest of the fall season, stomachs sampled across all cruises were empty.

PSL collected in the spring had varying stomach fullness ratios, averaging at 1.2. Most stomachs were empty; however, some fish had stomach contents (Figure 8). PH sampled in the spring exhibited feeding behavior as well (Figure 9). The observed mean stomach fullness during the spring was lower than during the fall.

Discussion:

Diet composition:

Pacific sand lance this year appeared to be eating primarily amphipods. This is inconsistent with past PEF findings, (Heller 2012, Burke 2014, Cieri 2015) and even with past research on diet in SJA (Miller 1980) that PSL primarily fed on calanoid copepods. Interestingly, the prey field in fall 2016, 2015, and perhaps other years, was dominated heavily by calanoid copepods. In past years, Pacific sand lance were assumed to be generalist feeders that took advantage of the large number of copepods available within the prey field. In 2016, PSL appear to have shifted away from the a generalist feeding strategy to a more selective strategy, choosing to feed largely on the amphipod population, which only comprised 6% of the prey field. This apparent selectivity is unexpected and could be due to shifts in the available prey at Jackson Beach as a result of lower copepod abundance overall in 2016 (Carter 2016) or due to the relatively small sample size in this location (N=15) compared to previous years (N=low-high Emily/Charlie/Alicia/Katie). Following this rationale, it may be that calanoid copepods, though relatively abundant were not at sufficient densities to sustain forage fish diets, leading to a relatively large reliance on amphipods this year compared to past years. It is important to note that the amount of fish caught this year were anomalously low (Huber 2016), and could have affected the observed results. The remaining few fish may have been the only fish able to shift to an amphipod focused diet.

The observed amphipods were not able to be identified to species. Evidence shows that hyperiids include species that are pelagic and those that are benthic. Understanding whether this prey source was primarily of benthic or pelagic origin important to understanding energy pathways in system and relative productivity in this system in context of anomalous conditions.

My finding, that the Pacific herring sampled from the dock had a diet consisting of about two-thirds copepod, is not consistent with data from 2014 where PH had been eating calanoid copepods in a much larger proportion (Burke 2014). It is important to note that previous samples were taken at Jackson Beach, rather than the dock. While the prey fields were similar, differences in diet composition could be a result of spatial variation and differences in sampling location. The dock has a different structure than Jackson Beach that could be conducive to the observable diet composition of PH sampled there. Alternatively, this increase in relative diet comprised of amphipods in Pacific herring (2016) and Pacific sand lance (2016 JB) may be reflective of a prey field that was more abundant in amphipods or more depleted in calanoid copepods, a primary food source for both species.

Surf smelt were much more generalist feeders than PH and PSL. 88% of the SS sampled from Jackson Beach consisted of calanoid copepods, which closely matches the prey field in zooplankton samples. While PSL focused on a small portion of the available prey field, SS took advantage of the more readily available copepod population. SS may be able to take advantage of this population due to their differing life strategy when compared to PSL. If prey density is a limiting factor, surf smelt that are more efficient in movement within the pelagic zone may be able to manage with reduced copepod densities. This may be further facilitated by the fact that the surf smelt sampled were of larger body size and ability to move in pelagic environments is directly correlated to body size (Sfakiotakis 1999).

The noticeable overlap in diet among these three species suggests they may be competing for calanoid copepods. All fish appear to be, to some extent, deriving a significant portion of diet from calanoid copepods. PH and SS appear to be mostly generalist feeders while PSL appeared to be selective. Combined with the low zooplankton abundance observed in 2016, this opens up the possibility of elevated levels of competition on calanoid copepods between these species of forage fish at Jackson Beach. Studies performed on interspecific interactions between two other forage fish, the common roach and the surf perch, suggest that the presence of competing species causes change in growth rate, population, and diet composition (Persson 1986). Because of this, the interspecific relationship between the three forage fish species studied this year could be causing changes in nutrient uptake by PSL. Also of note, this is the first year in nearshore sampling that has noted sustained presence of surf smelt in net tows at Jackson Beach.

As SS diet is not well studied in PEF, future studies should focus on obtaining a larger data set for SS diet composition and fine scale shifts in the plankton population at this location. This will help determine if the change in PSL diet observed in 2016 is due to competition or simply variations in prey field. Additionally understanding condition in multiple fish species (PSL, PH, SS) across years and comparing these samples to other more comprehensively sampled species (e.g., juvenile salmonids) would further strengthen linkages between physical environment, prey fields, diets, forage and condition.

Spatial Variation:

The diet composition observed in PSL from Jackson Beach and PSL from South Beach differs greatly. While fish from Jackson Beach had almost half of their diet consisting of amphipods, the South Beach fish diet consisted of mainly calanoid copepods and their nauplii. In order to explain this difference in diet, it is important to note the differences between the two sites. Jackson Beach lies within San Juan Channel and in an enclosed bay (Figure 1), protected from wave activity. This allows for a more diverse benthos to exist, creating a favorable habitat for plankton such as amphipods. South Beach is located on the south side of San Juan Island, open to the wave activity from the Salish Sea. The benthos is not favored here, meaning the prey field for PSL is limited to pelagic plankton such as calanoid copepods. The difference in composition between the two locations can likely be attributed to differences in habitat affecting available prey. Fish at South Beach are consuming calanoid copepods in a greater proportion than PSL at Jackson Beach because they are more abundant than benthic plankton.

The other locations sampled, Iceberg Point and Salmon Bank, did not have any actively feeding fish. The fish sampled were presumed to be adult fish that had already entered their winter dormancy. Similar to the Jackson Beach-San Juan Channel wave field, the presence of young nearshore fish that are feeding compared (JB) to adult fish that are hibernating (SJC) indicates the possibility of an analogous relationship between South Beach-Salmon Bank and some other near shore location-Iceberg Point. There is potential for nearshore PSL at South Beach and Lopez Island to be migrating out towards the off shore wave fields present there. Future studies should tag fish or take genetic samples to determine if this relationship is present.

Stomach Fullness:

Over the course of the fall season, there was no observable feeding activity in San Juan Channel. Except for the one outlier found in the sample from the first cruise, all the adult offshore fish sampled had entered winter dormancy While in past years, studies had noted a decline in stomach fullness over the course of the fall season, in 2016 PSL in the San Juan channel appeared to enter their winter dormancy in early October. While that seasonal decline in stomach fullness was noted in past PEF researchers (Rood 2010, Highland 2013, Heller 2012) the 2016 trend is consistent with last year's findings (Cieri 2015) that describe a similar trend in early winter dormancy in offshore locations. Previous research shows that the fish begin their dormancy sometime in early October, with a steady decrease in mean stomach fullness over the fall season. PSL in 2015 and 2016 entered this inactive period earlier than previous years.

This shift in the timing of the winter dormancy could be potentially due to the presence of the marine heat wave. Elevated temperatures are known to increase metabolism in teleost fish (Johnston 1987). If the levels of production in San Juan Channel decrease with decreasing light levels, the PSL would not be able to support the energy costs of foraging. Fish cannot regulate their internal body temperature, often choosing to migrate to deeper, colder water (Walberg 2011). In order to avoid the stress created by the marine heat wave, PSL could have migrated down to the bottom and entered dormancy prematurely. Also, the timing of the fall transition in 2016 was pronounced and earlier than in past years (Smith 2016). While the fall transition (Mid October) occurred after our initial sampling of fish in the SJC (October 4, Mid October), the earlier onset of fall transition, which reflects move from upwelling to downwelling may reflect a suite of oceanographic patterns relevant for foraging.

Another component of diet analyses examined this year that was novel was seasonal comparison, facilitated by samples collected in the spring of 2016. In comparisons across seasons, Pacific sand lance caught in the spring showed apparent feeding activity. Although low, some of the PSL sampled on February 27th exhibit feeding behavior, and while the stomachs of the feeding fish were not full, contents still appeared within the gut. This means that the fish are beginning to leave winter dormancy and enter their active feeding period for the spring and summer. Knowing that winter dormancy has occurred sometime before early October and is ending sometime near the end of February, a timeline for the period of winter dormancy can be established. Looking at the timing of feeding behavior, the winter dormancy period can be assumed to be between early October and early February. The timing of the spring bloom occurring as a result of the transition back from downwelling to upwelling could be a possible driver for the fish to resume feeding activity.

The seasonal changes in Pacific herring indicates that these fish are still exhibiting feeding behavior all year. As a result, variations in stomach fullness are assumed to be due to difference in availability of prey, rather than the choice to forage or not.

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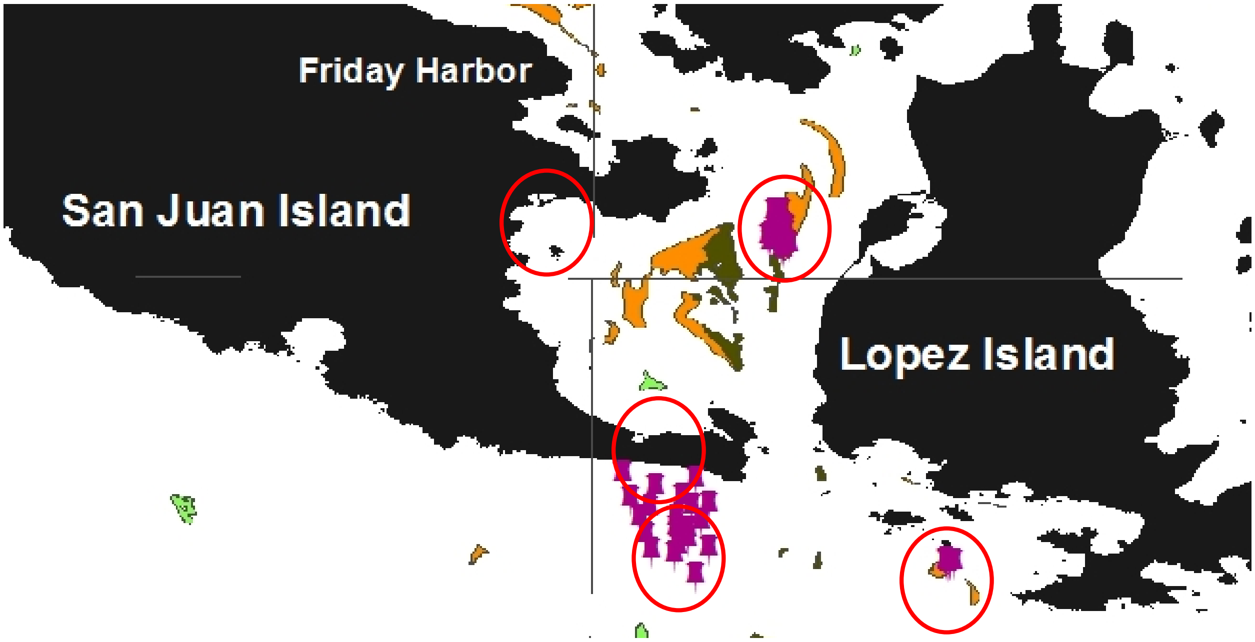

Figure 1: Map of sample sites for fall 2016. Site where fish were caught are circled in red

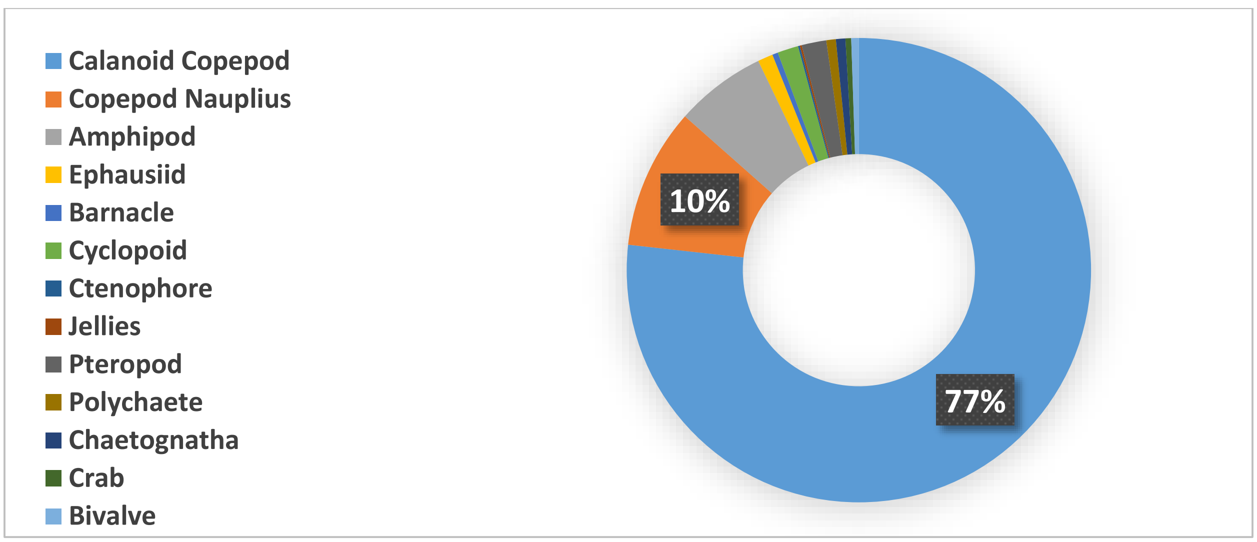

Figure 2: Prey field at Jackson Beach

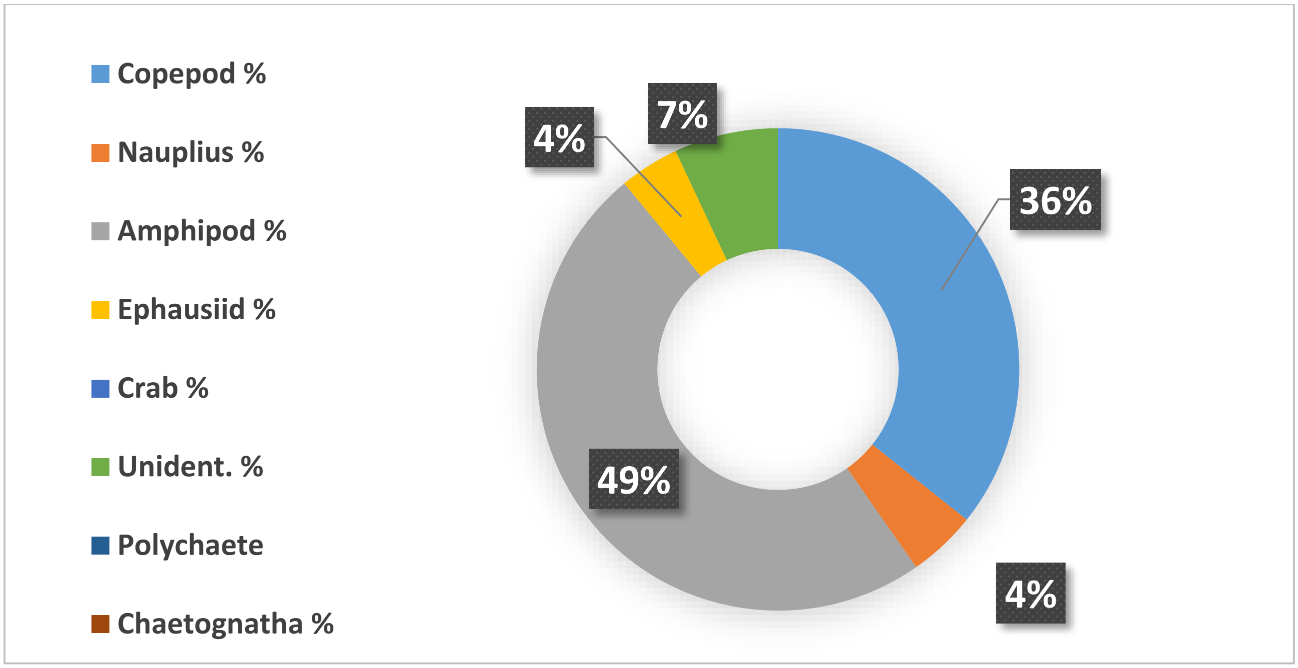

Figure 3: Proportional PSL diet at Jackson Beach

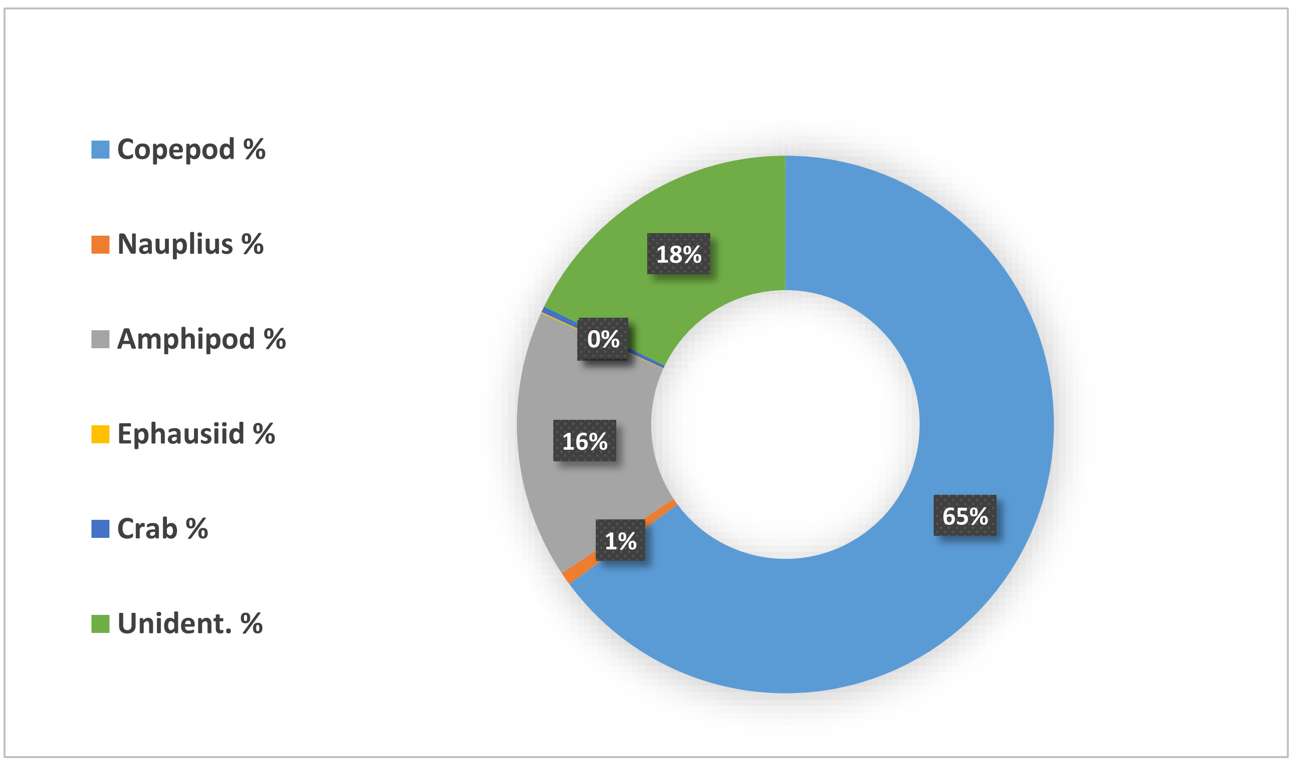

Figure 4: Proportional PH diet from FHL dock

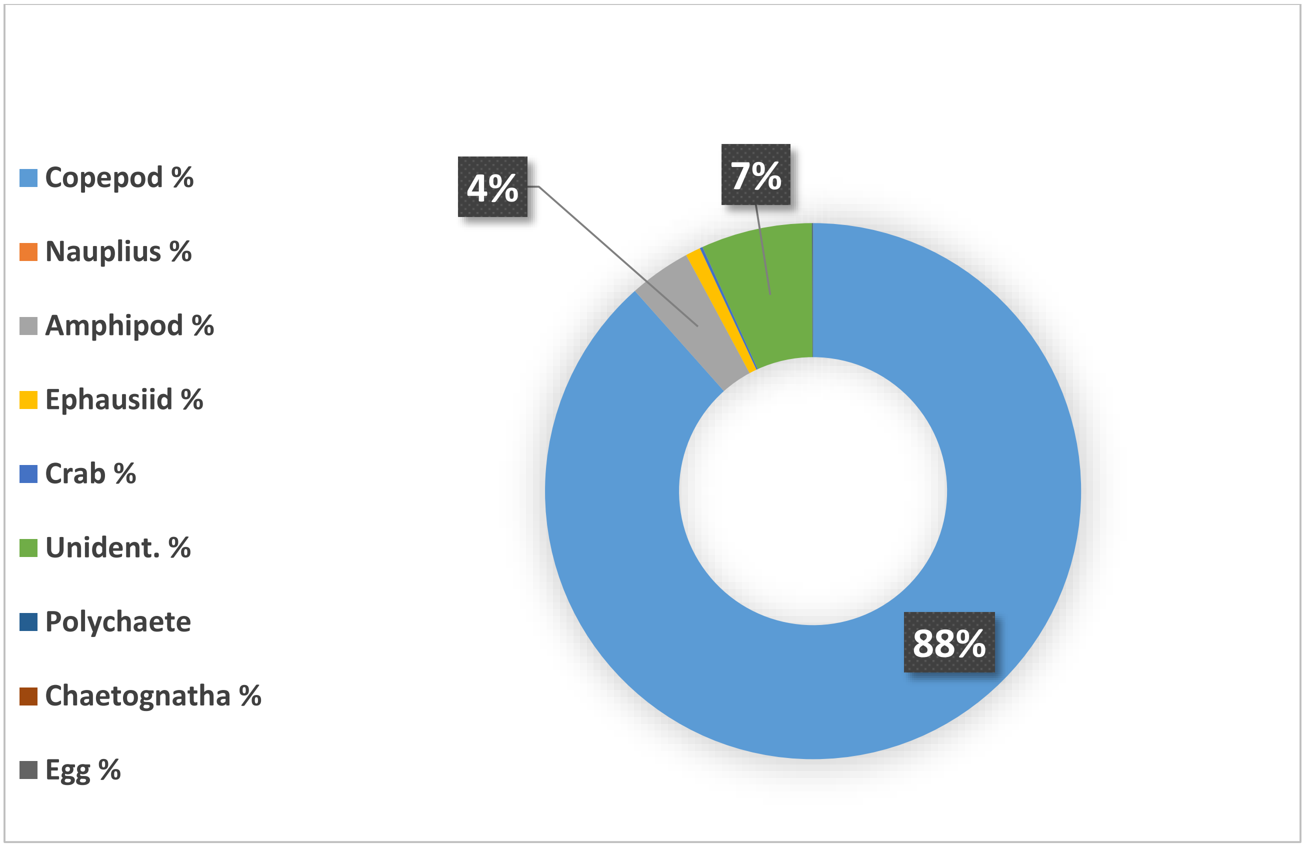

Figure 5: Proportional Surf smelt diet at Jackson Beach

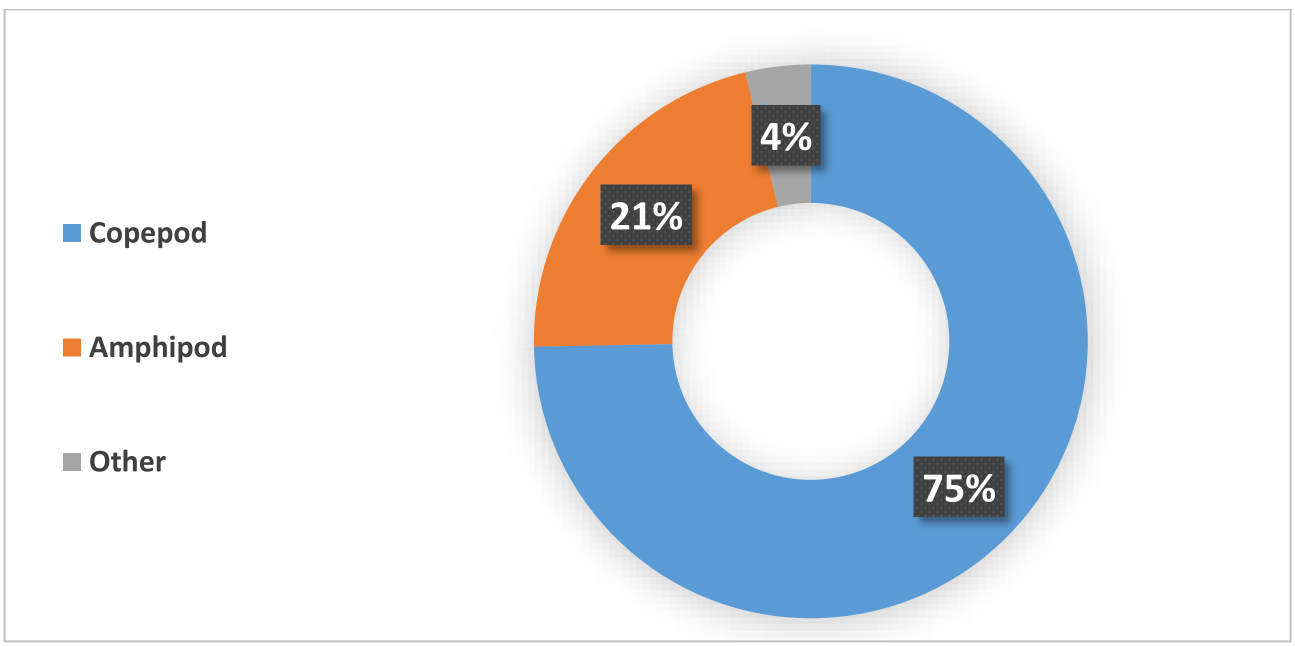

Figure 6: Proportional diet of PSL at South Beach

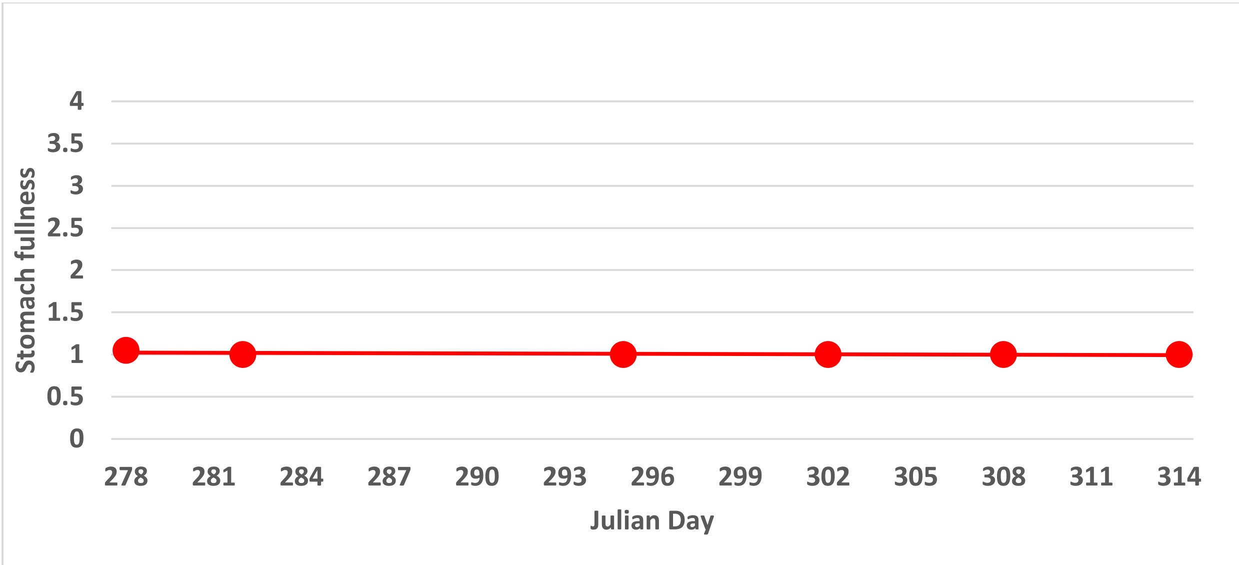

Figure 7: Mean stomach fullness over fall 2016 sampled from San Juan Channel

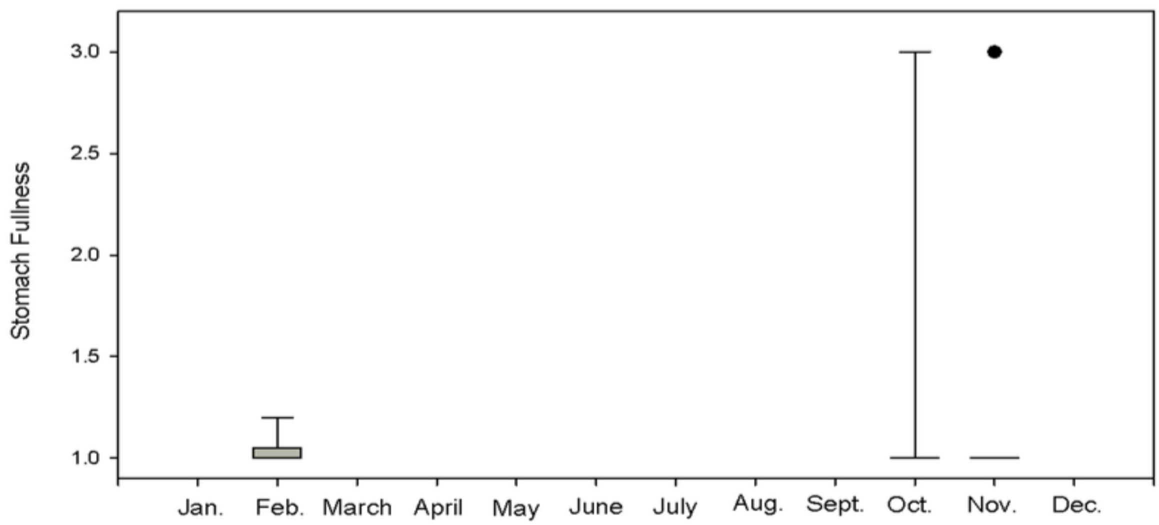

Figure 8: Mean stomach fullness for all spring and fall PSL data from San Juan Channel

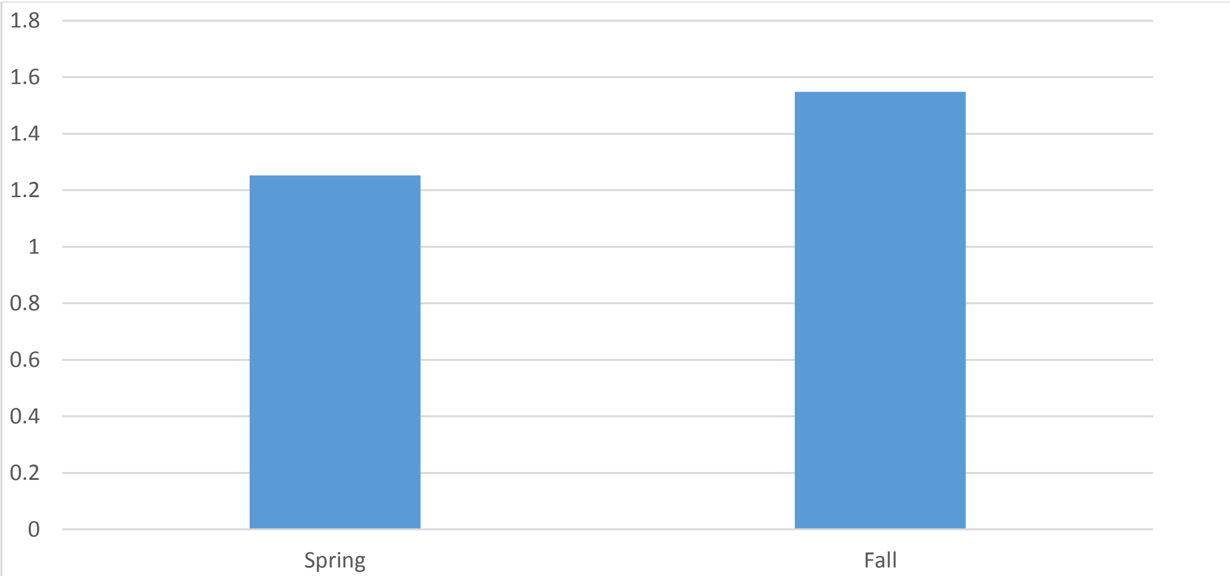

Figure 9: Stomach fullness ratio for spring PH compared to fall PH sampled from FHL dock