Feeding ecology of forage fishes in the San Juan Archipelago: Diet composition and variation in *Ammodytes hexapterus, Hyperprosopon ellipticum,* and *Clupea pallasii*

Emily A. Burke[1]

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

Contact information:

Emily A. Burke

emilyalanaburke@gmail.com

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ABSTRACT

Forage fish play an important role in wasp-waist ecosystems like that of the San Juan Archipelago. These small fish, including the Pacific sand lance, silver surf perch, and Pacific herring, regulate the flow of energy through the trophic levels of this marine ecosystem, from the plankton to the larger predatory fish, sea birds, and marine mammals. Gut content analyses reveal that Pacific sand lance and Pacific herring feed primarily on calanoid copepods, while the surf perch has a more varied diet. Pacific sand lance and Pacific herring had low values on Levins' standardized measure of niche breadth, indicating a narrow dietary breadth characteristic of a specialized diet. Surf perch had a higher value, indicating a wider dietary breadth and more generalist feeding approach. Morista's measure of niche overlap was used to quantify dietary overlap between the species. Pacific sand lance and Pacific herring had a high rating, which could indicate competition for the same prey items. Both of these species' dietary overlap with surf perch was much lower, suggesting little competition for prey items. The diet composition of surf perch exhibited significant temporal variation. The diet composition of Pacific sand lance did not exhibit significant temporal variation, but did exhibit significant spatial variation between Jackson Beach and the sand wave channel. By quantifying these measures of compositional, temporal, and spatial variation in forage fish diets, we can now better understand the types of resource partitioning that are influencing trophic exchange in the San Juan Archipelago.

INTRODUCTION

Wasp-waist control of energy flow in marine ecosystems occurs when a small number of species can sequester and control much of the energy flow between the lower and upper trophic levels (Hunt and McKinnell 2006). Forage fish play an important role in wasp-waist-controlled ecosystems like that of the San Juan Archipelago (Bakun 2006). Small forage fish, primarily the Pacific sand lance, silver surf perch, and Pacific herring, regulate the flow of energy through the trophic levels of this marine ecosystem, from the plankton to the larger predatory fish, sea birds, and marine mammals. As mid-trophic predators, forage fish exert top-down control on the plankton community and simultaneously, due to their limited numbers, they exert bottom-up control on upper-level predators that rely on the forage fish to fill meet nutritional needs (Cury *et al.* 2000).

Forage fish in the San Juan Channel differ in life history strategy and feeding ecology. Pacific sand lace (PSL) spend much of their lives buried in sandy substrate but come up into the water column to feed, primarily on calanoid copepods (Hipfner and Galbraith 2013, Highland 2013, Haynes *et al.* 2007, Robards *et al.* 1999, Hobson 1986). Surf perch (SP) are pelagic fish that feed in near-shore waters on a variety of prey types, including amphipods, isopods, decapods, euphausids and mysids (Holbrook and Schmitt 1992). Pacific herring (PH) are entirely pelagic fish and widely considered to be among the most abundant prey species in the San Juan Archipelago. The diet of juvenile PH is primarily composed of calanoid copepods, decapod larvae, and chaetognaths, but has been shown to vary spatially and seasonally (Foy and Norcross 1999).

Partitioning food resources can promote coexistence among otherwise similar species. Thus, comparisons of feeding ecology, specifically diet composition and variation, are critical to understanding the relationships among forage fish species (Sturdevant 2000). Resources, in this case potential prey, can be partitioned in many ways, including by composition, temporally, and spatially. For example, when two species consume different prey items they are partitioning their food resources by composition. High dietary overlap, occurring between species with similar prey preferences, could result in either spatial or temporal partitioning. Spatial partitioning occurs when species feed in distinct geographic areas and temporal partitioning occurs when species feed at different times. All three of these varieties of resource partitioning may increase tolerance of niche overlap, thus reducing competition for prey items between co-occurring species (Holbrook and Schmitt 1989).

Understanding these details of forage fish feeding ecology can place mechanisms of population control throughout trophic levels in a wider context and demonstrate their influence on how these populations respond to environmental perturbations (Hunt and McKinnell 2006). Energy transfer between trophic levels can also help explain pelagic ecosystem function in the San Juan Archipelago, such as the links between phytoplankton and zooplankton through the forage fish at the center of the wasp-waist ecosystem and up to larger predatory fish, sea birds, and marine mammals.

This study aimed to examine the diet composition and variation of three species of forage fish: Pacific sand lance (Ammodytes hexapterus), silver surf perch (*Hyperprosopon ellipticum*), and Pacific herring (*Clupea pallasii*). The study goals were to determine the dietary composition and breadth of each species as well as measure the dietary overlap between species. In addition, this study investigated if and how the diet composition of each species (1) changed throughout the fall and (2) varied between collection sites. By quantifying these measures of compositional, temporal, and spatial variation in forage fish diets, allows us to better understand the processes of resource partitioning governing trophic exchange in the San Juan Archipelago.

METHODS

I. Study Site

All specimens were collected from the San Juan Channel (San Juan Archipelago, WA, USA) between September and November 2014. The two primary sampling sites were Jackson Beach (48.5196N, 123.0082W) and the sand wave field (approx. 48.5125N, 122.9540W) (Figure 1).

II. Jackson Beach Collection

Specimens were collected at Jackson Beach throughout the fall season using small boats and a beach seine. In this technique, one end of the net is held in place on shore while the small boat deploys the rest of the net in a large arc until the other end is back on the shore. While slowly pulling the net towards shore from either end, organisms are captured in the narrow-diameter cod end as the lead-weighted bottom of the net scrapes along the substrate and the buoyed top of the net prevents fish from escaping near the surface. Bycatch, including sculpins, tubesnouts, sticklebacks, crabs, shrimp, and nudibranchs, were immediately released while Pacific sand lance, surf perch, and Pacific herring were kept for further analysis. Specimens from a variety of seining collection events were included in this study, including seines on October 1st, 6th, 8th, 18th, and 24th.

III. Sand Wave Field Collection

Specimens were collected at the sand wave field throughout the fall season using a Van Veen grab from the *RV Centennial*. The Van Veen grab collects the both Pacific sand lance and the sediment in which they are buried by collapsing and scooping sediment when the instrument hits the seafloor. Specimens included in this study were collected from Van Veen grab collection events on September 30th, October 7th, 14th, and 21st. Pacific sand lance continued to be collected on weekly *RV Centennial* cruises through November 10th, however none of the specimens contained any gut contents on which analyses could be conducted.

IV. Laboratory Preparation

Specimens were euthanized with a lethal dose of tricaine methanesulfonate (MS-222), a poikilotherm anesthetic, and preserved in a 10% formalin solution (Highland 2013, Heller 2012). The specimens were measured and weighed for historical records and for studies focusing on distribution and abundance. Their stomachs were extracted and fixed in a formalin solution for later analysis.

V. Gut Content Analysis

Gut contents were examined under a dissecting scope and prey items were identified to the lowest possible taxon. Prey items were quantified using methods such as numeric method 1 (NM1) and frequency of occurrence (FO), both recommended for gut content analysis by Ahlbeck *et al.* (2012). In NM1, prey percentages were calculated for each individual fish before averaging over all the individuals in that sample **(Hyslop 1980).** This method gives equal weight to every fish, regardless of other factors such as fish size or stomach fullness.

Numeric method 1 (NM1):

$$\mathrm{Diet}_i^{\mathrm{NM1}} = \frac{\sum_{j=1}^{N_{\mathrm{fish}}} \left(\frac{N_{ij}}{N_{\bullet j}} \times 100 \right)}{N_{\mathrm{fish}}}$$

Where $\mathrm{Diet}_i^{\mathrm{NMI}}$ = Mean percentage of prey type *i* in the diet

N_{fish} = Number of fish examined

N_{ij} = Number of prey type *i* in individual *j*

N_{*j} = Total number of prey in gut of individual *j*

To calculate FO, the proportion of stomachs containing each prey type was calculated for each sample group and expressed as a percentage of the total number of stomachs (Ahlbeck *et al.* 2012).

<u>*Frequency of occurrence:*</u>

$$\mathrm{Diet}_i^{\mathrm{FO}} = \frac{N_{\mathrm{fish},i}}{N_{\mathrm{fish}}} \times 100$$

Where $\mathrm{Diet}_i^{\mathrm{FO}}$ = FO of prey type *i* in the diet

$N_{\mathrm{fish},i}$ = Number of fish containing prey type *i* in their gut

N_{fish} = Number of fish examined

These values were then used to derive a dietary breadth measure and a dietary overlap index. The significance of temporal and spatial variance as differences in individual categories were evaluated on the basis of t-tests, and differences in overall diet ratios were evaluated via an analysis of similarities used to test for significant differences between one or more categories (ANOSIM; Clarke 1993). Data was evaluated in R (Package ANOSIM {vegan}; Oksanen *et al.* 2014).

VI. Dietary Breadth

Dietary breadth was calculated using Levins' standardized measure of niche overlap. This measure, first suggested by MacArthur and Levins (1967) is used to understand diet specialization and ranges from 0 to 1.0, where values close to 0 indicate specialization while values close to 1.0 indicate generalization.

<u>*Levins' Measure of Niche Breadth:*</u>

$$B = \frac{1}{\Sigma p_i^2}$$

Where B = Levins' measure of niche breadth

p_i = Proportion of individuals recorded from prey item class *i*

Levins' Standardized Measure of Niche Breadth:

$$B_A = \frac{B - 1}{N - 1}$$

Where B_A = Levins' standardized measure of niche breadth

B = Levins' measure of niche breadth

N = Number of prey item classes

VII. Dietary Overlap

Dietary overlap was calculated using Morista's measure of niche overlap (Morista 1959). This measure is used to understand diet overlap between two species and ranges from 0 to 1.0, where values close to 0 indicate no overlap while values close to 1.0 indicate near complete overlap. This measure is useful in evaluating interspecific relationships, as high levels of dietary overlap suggest competition over the prey items.

Morista's Measure of Niche Overlap:

$$C = \frac{2\Sigma\, p_{ij}\, p_{ik}}{\Sigma p_{ij}\left[\frac{n_{ij} - 1}{n_j - 1}\right] + \Sigma p_{ik}\left[\frac{n_{ik} - 1}{n_k - 1}\right]}$$

Where C = Morista's index of niche overlap between species *j* and *k*

p_{ij} = Proportionate occupation of prey type *i* by species *j*

p_{ik} = Proportionate occupation of prey type *i* by species *k*

n_{ij} = Number of individuals of species *j* that occupy prey type *i*

n_{ik} = Number of individuals of species *k* that occupy prey type *i*

n_j = Number if individuals of species *j*

n_k = Number if individuals of species *k*

RESULTS

I. Diet Composition

Pacific sand lance (PSL) was found to have a fairly homogenous diet (Figures 2 and 3). The seasonal mean of 30 individuals was dominated by calanoid copepods (83.93% of prey count, 100% FO) and amphipods (6.28% of prey count, 84% FO). Less prevalent prey items included cyclopoid copepods, copepod nauplii, barnacle nauplii, decapods, eggs, larvaceans, and mites. On a scale from 0 to 1, PSL had a dietary breadth value of 0.029. Also on a scale from 0 to 1, PSL had a dietary overlap value of 0.1973 with SP, and 0.7918 with PH.

Surf perch (SP) was found to have a more varied diet (Figures 4 and 5), The seasonal mean of 22 individuals was dominated by of isopods (19.88% of prey count, 73% FO), euphausids and mysids (18.7% of prey count, 95% FO), calanoid copepods (17.17% of prey count, 77% FO), ostracods (11.66% of prey count, 77% FO), and amphipods (5.21% of prey count, 54% FO). Less prevalent prey items included eggs, decapods, barnacle larvae, harpacticoid copepods, larvaceans, pleuteus larvae, mites, copepod nauplii, and cyclopoid copepods. On a scale from 0 to 1, SP had a dietary breadth value of 0.516. Also on a scale from 0 to 1, SP had a dietary overlap value of 0.1973 with PSL, and 0.1970 with PH.

Pacific herring (PH) was found to have a fairly homogenous diet (Figures 6 and 7). The seasonal mean of 12 individuals was dominated by calanoid copepods (85.3% of prey items, 100% FO) and amphipods (7.41% of prey count, 58% FO). Less prevalent prey items included ostracods, decapods, euphausids and mysids, eggs, copepod nauplii, larvaceans, chaetognaths, and cyclopoid copepods. On a scale from 0 to 1, PH had a dietary breadth value of 0.026. Also on a scale from 0 to 1, PH had a dietary overlap value of 0.7918 with PSL, and 0.1970 with SP.

II. Temporal Variation

The 2014 fall transition was determined by the PEF oceanography team to be approximately October 17^{th}. This date was used to group specimens into pre-transition and post-transition collection groups on which statistical analyses were run.

No significant temporal variation was found in the diet composition of PSL before and after the fall transition. There was, however, a major change throughout the fall in relation to the presence or absence of prey items. After October 29th, no PSL were collected that contained any prey items in their stomach.

Significant temporal variation was present in SP diet. Pre-transition, SP diet was dominated by a variety of prey items (Figure 8). Post-transition, SP diet composition exhibited a significant increase in the proportion of euphausids and mysids ($p = 0.0085$) and significant decreases in the proportion of calanoid copepods ($p < 0.0001$), isopods ($p < 0.0001$), and amphipods ($p < 0.0001$) (Figures 9 and 10). This significance was confirmed via ANOSIM ($R = 1$, $p = 0.001$).

III. Spatial Variation

Significant spatial variation was found in PSL diet between Jackson Beach and sand wave field collection sites (Figures 11 and 12). Diet composition showed a significant increase in the proportion of amphipods ($p = 0.0082$) and a significant decrease in the proportion of calanoid copepods ($p = 0.0139$). This significance was confirmed via ANOSIM (R = 1, p = 0.001). A generalized summary of all analyses conducted in this study can be found in the appendix of this paper (Table 1).

DISCUSSION

I. Diet Composition

The diet composition of Pacific sand lance (PSL), surf perch (SP), and Pacific herring (PH), were consistent with findings from previous research (Highland 2013, Hipfner and Galbraith 2013, Foy and Norcross 1999, Holbrook and Schmitt 1992). The similar diets of PSL and PH are interesting because they suggest that, despite different life history strategies and feeding ecologies, both PSL and PH rely heavily on calanoid copepods. While the diet compositions of PSL and PH have been examined separately, this was the first comparative study conducted in the San Juan Archipelago. The high dietary overlap value between PSL and PH confirms their similar diet preferences and could indicate increased levels of competition over calanoid copepods.

Calanoid copepods and copepod nauplii dominated the plankton composition in the San Juan Channel throughout the fall (Zayas del Rio 2014). Due to differences in percent composition of zooplankton types between the water column and the gut contents of fish, it may be assumed that generally these species are searching out specific prey items, not opportunistically feeding on a random sample of prey from the water column. This is especially clear from prey items with low pelagic occurrence that appear in high numbers and percent composition of certain diets (*e.g.* isopods in SP diet). Future studies should build off this research by examining the fine-scale variation in plankton composition throughout the collection sites in the San Juan Channel and compare the findings to fine-scale variations in forage fish diets. This would quantify the selectivity of the diets and confirm previous assumptions by placing them in the context of the plankton composition in their specific collection site.

The large dietary breadth of SP indicates a more generalist feeding approach that relies on a variety of prey items, confirming the results of previous studies. This study, however, combined both breadth and diet proportion analyses to reveal that SP not only consume a variety of prey items, but rely on many of them, as the variety of prey items make up large and near-equal proportions of their diet. This is interesting because while the content of SP diet has been studied, the composition proportions have not received the same attention. By continuing to study SP diet, future research could study how SP diet is influenced by physical oceanography factors, such as temperature and salinity, and biotic factors, such as plankton availability. SP diet had low levels of overlap with PSL and SP diets, suggesting little competition for prey items and consistent with discussions of how resource partitioning can lower competition between species.

II. Temporal Variation

Seasonal change may affect the various species differently because of their distinct foraging habits. SP, the more generalist forager, had more prey options on which to rely throughout the changing season. SP diet composition exhibited significant temporal variation. After the fall transition, SP diet underwent a major composition shift from many types of prey to being dominated by euphausids and mysids. This could indicate a shift away from a more generalist diet towards a more efficient way of obtaining energy, as two or three large euphausids or mysids would fill the stomach as much as a mixture of several hundred smaller isopods, ostracods, and calanoid copepods.

Future studies could look into the intricacies of nutritional content of various prey items and their effect on diet as a whole. By continuing to study SP diet over longer periods of time, future studies could also examine how SP diet is influenced by temporal variation in physical oceanography and biotic factors.

No significant temporal change was found in PSL diet composition. There was, however, a major change in presence or absence of prey items. After October 29th, no PSL were collected that contained any prey items in their stomach. This is likely due to PSL's distinct behavior of burrowing in the substrate for the winter, which is consistent with previous studies observing that PSL stop feeding before this hibernation period, usually in the end of October (Heller 2012). Future studies could monitor this temporal shift on a targeted, finer scale.

III. Spatial Variation

The significant spatial variation found in PSL diet indicates that PSL diet is indeed influenced by location. When examined in the context of past research indicating age variation between study sites (Hipfner and Galbraith 2013, Heller 2012, Johnson *et al.* 2008, Robards *et al.* 2002,), these results could suggest that diet composition may also vary with age. If this is indeed the case, the population at Jackson Beach, generally smaller in size and thus considered younger by the Wyllie-Echeverria method (2010, unpublished data), would be consuming different proportions of prey than the larger and older population in the sand wave field.

Spatial diet variation in PSL is consistent with the findings of Highland (2013), who used stable isotope data to determine that PSL in the sand wave field and at Jackson Beach consume different proportions of prey items. The specimens collected in the sand wave field had a higher Nitrogen isotope signature, indicating higher trophic level feeding, and a higher Carbon isotope signature, indicating an offshore signal. Specimens collected at Jackson Beach had isotope signatures indicating nearshore and lower trophic level feeding. Overall this would suggest that PSL in different collection sites are feeding in separate areas. It is likely that there is one population of PSL that is separated spatially with habitats associated with different life stages.

The influence of age and location on diet composition would be an excellent area for future research, as understanding the dynamics of and connections between the Jackson Beach and sand wave field populations will help place the diet research of PSL into a larger context of PSL life history and its many roles in the pelagic ecosystem.

IV. Conclusions

From this study it can be observed that both inter- and intraspecific resource partitioning occurs in the diet of forage fish found in the San Juan Archipelago. Measures of dietary breadth and overlap confirmed predictions of feeding interactions between species, and temporal variation in diet composition was detected in surf perch diets, suggesting adaption to the feeding environment throughout the fall season. In addition, spatial variation was detected in Pacific sand lance diets, which is consistent with previous research on feeding differences between collection sites.

All of these dimensions – composition, temporal, and spatial – contribute towards the discussion of how partitioning prey resources can promote coexistence of similar species and increase tolerance of niche overlap by reducing competition for resources. This research has value for theoretical biology, specifically regarding inter- and intraspecific interactions, and fisheries management, such as decision making surrounding forage fish stocks. Understanding the dynamics of how forage fish interact with each other can be built upon by continuing to study how these fish link plankton to larger predators and influence pelagic ecosystem function in the San Juan Archipelago.

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APPENDIX

I. Figures

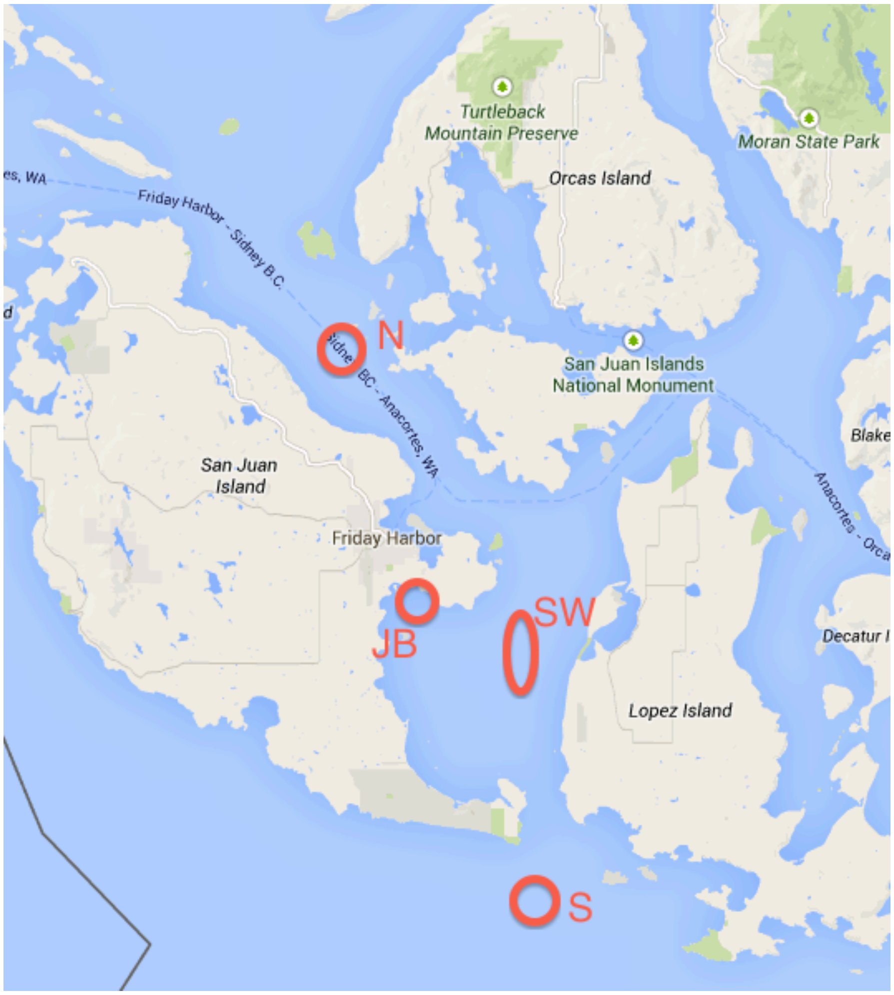


Figure 1. Sampling sites in the San Juan Archipelago. JB = Jackson Beach, SW = sand wave field, N = North Station, S = South Station. Base-layer map from GoogleMaps.

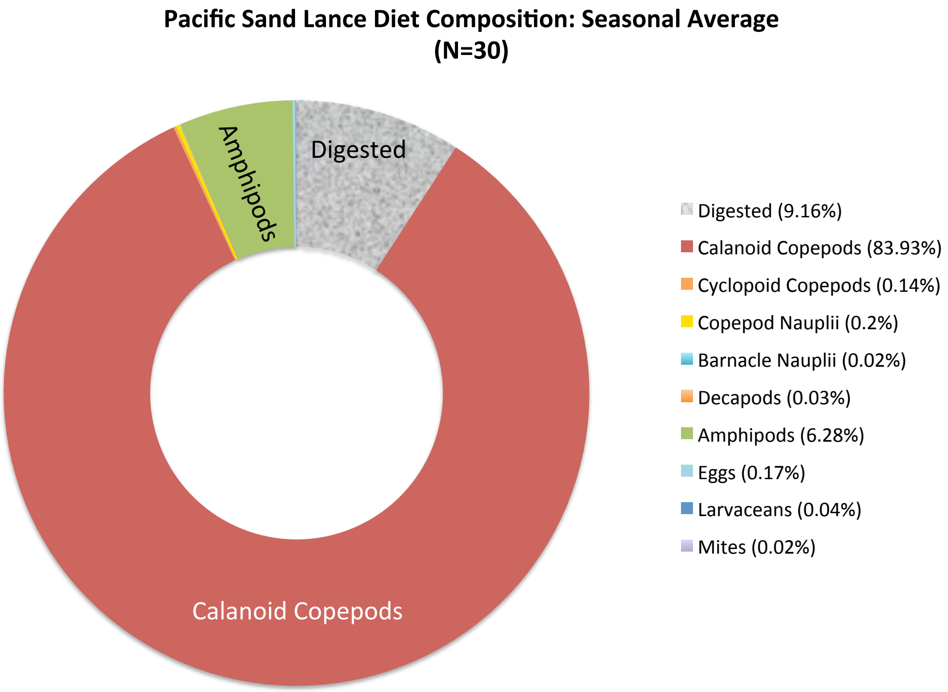


Figure 2. Seasonal average of PSL diet composition (N = 30).

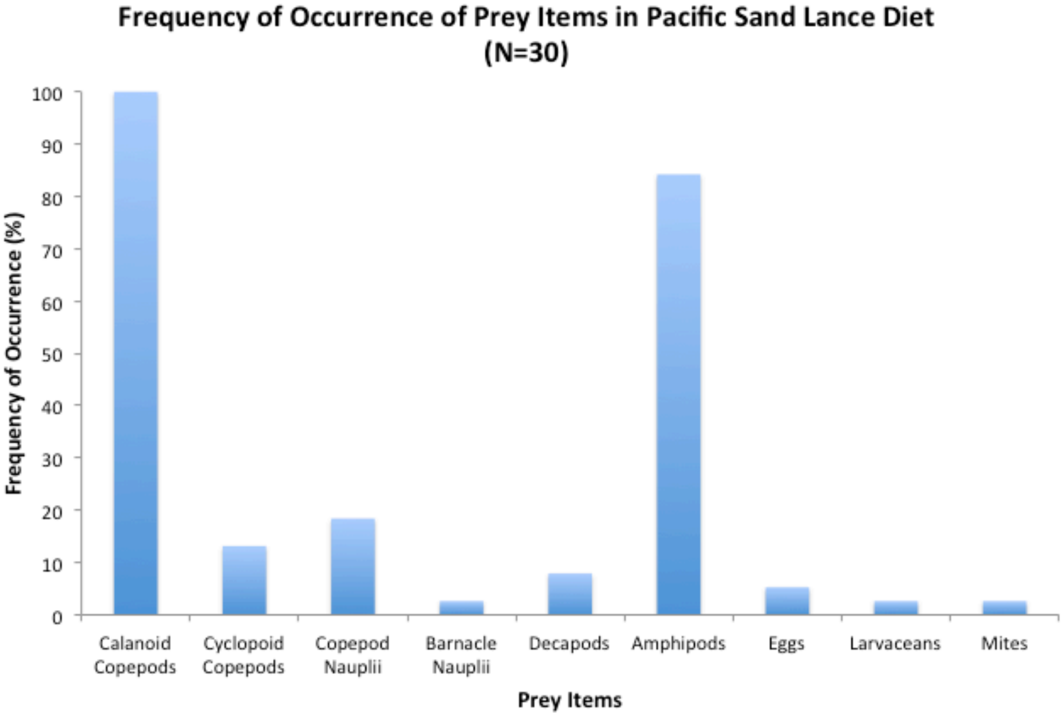


Figure 3. Frequency of occurrence of prey items in PSL diet (N = 30).

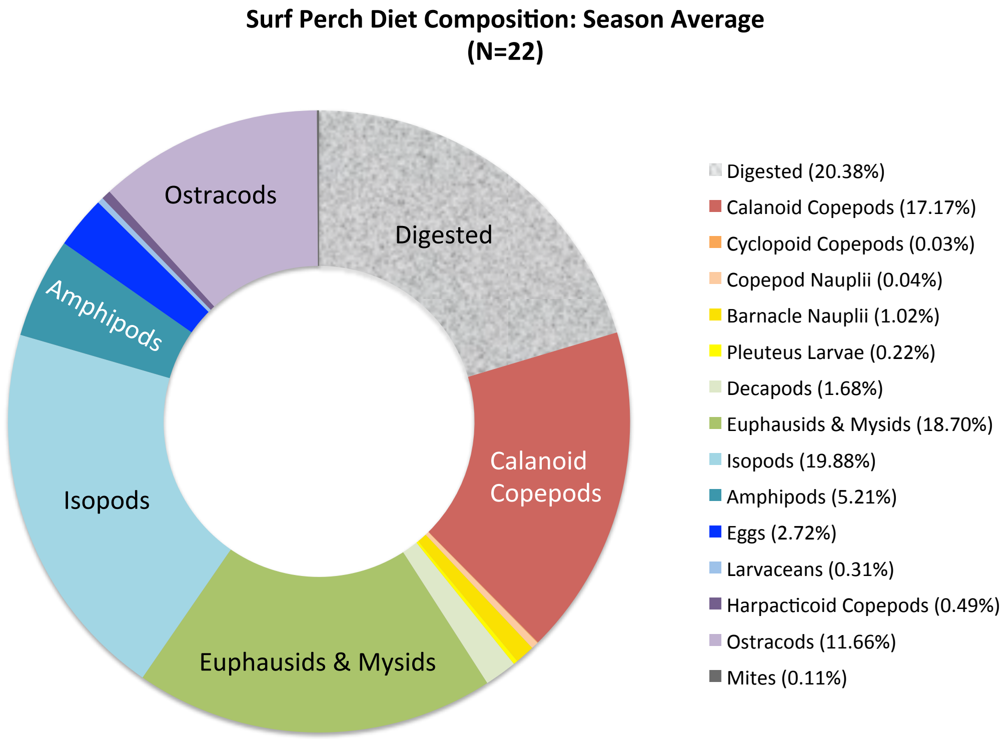


Figure 4. Seasonal average of SP diet composition (N = 22).

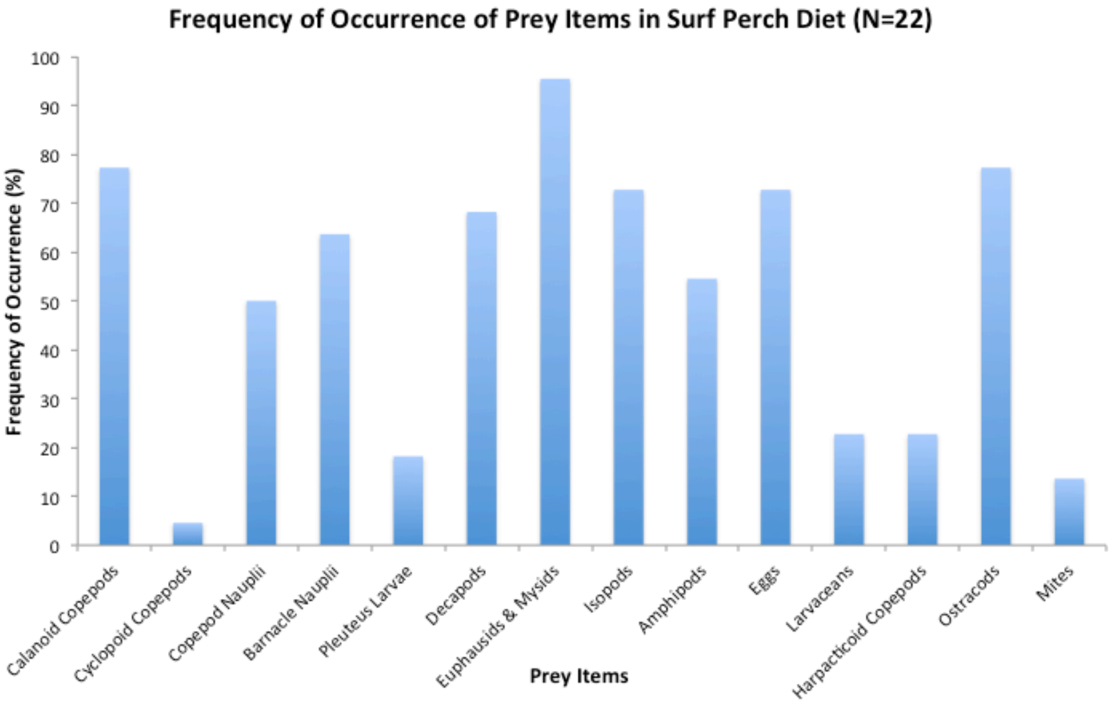


Figure 5. Frequency of occurrence of prey items in SP diet (N = 22).

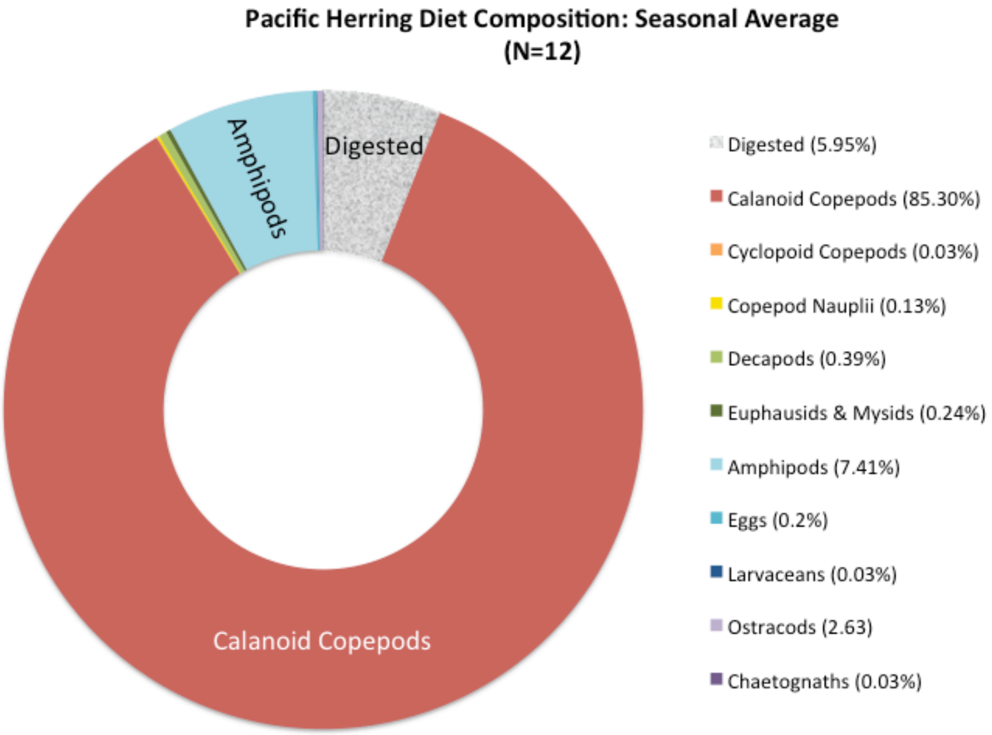


Figure 6. Seasonal average of PH diet composition (N = 12).

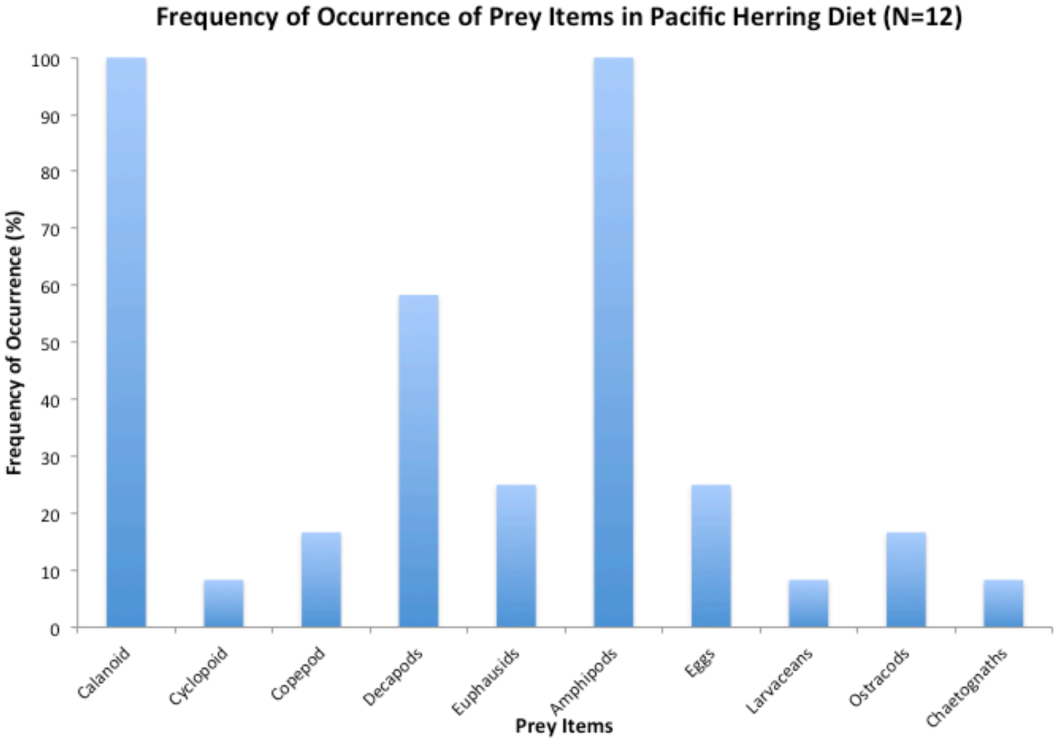


Figure 7. Frequency of occurrence of prey items in PH diet (N = 12).

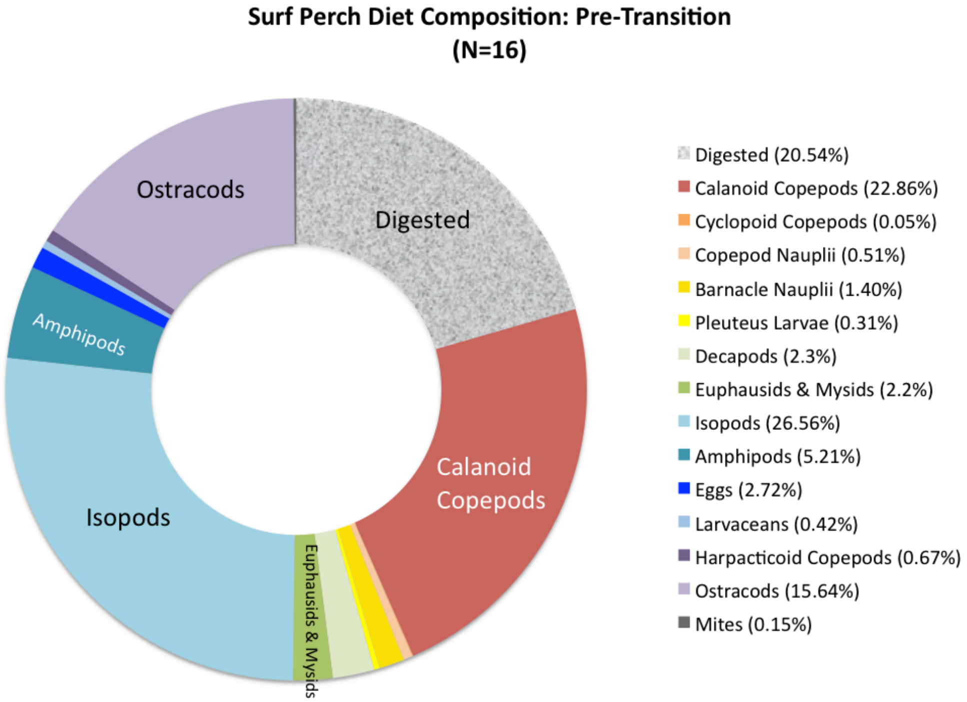


Figure 8. Pre-transition average of SP diet composition (N = 16).

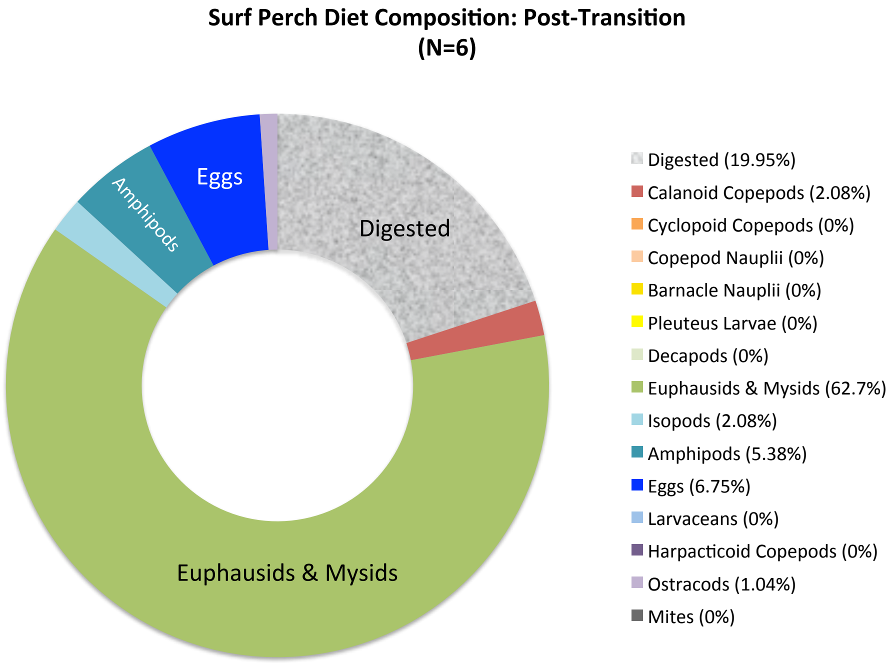


Figure 9. Post-transition average of SP diet composition (N = 6).

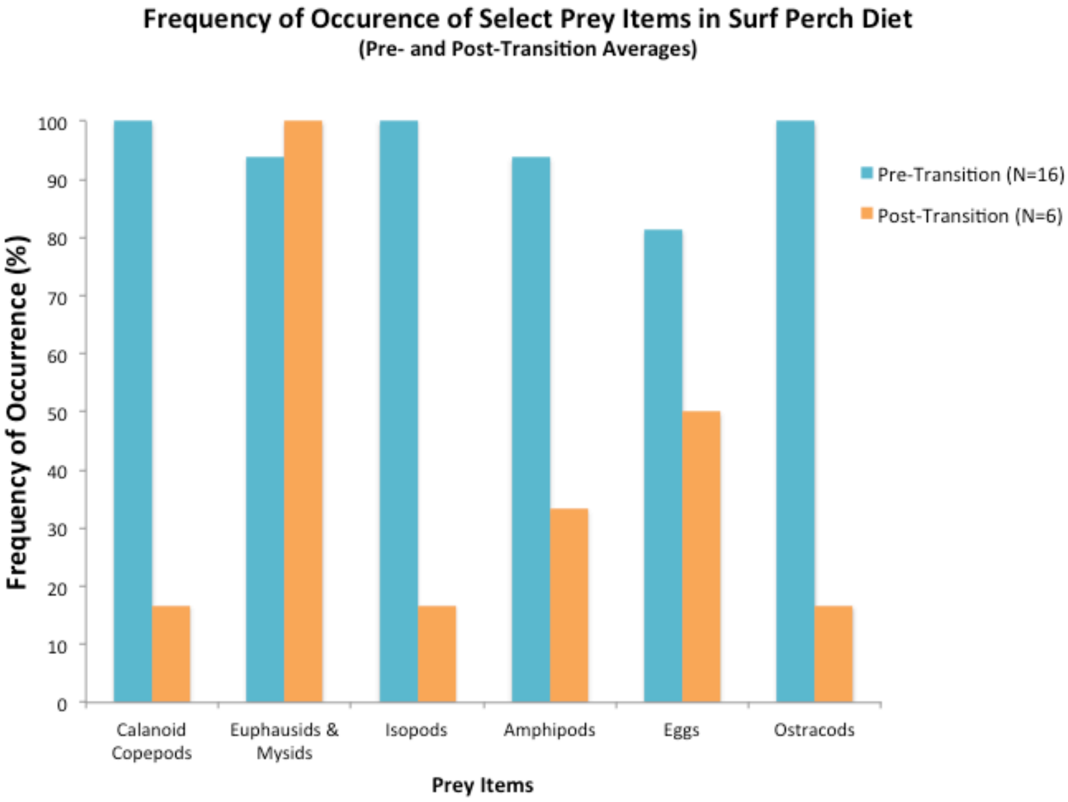


Figure 10. Frequency of occurrence of prey items occurring in both pre- and post-transition SP diets (N = 22).

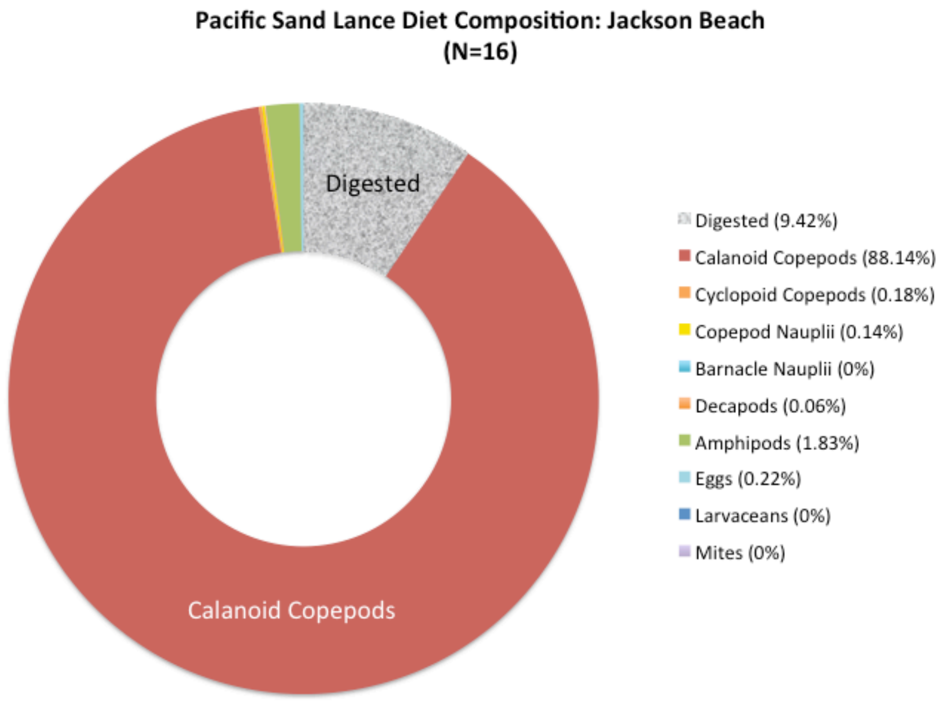


Figure 11. Seasonal average of SP diet composition at Jackson Beach (N = 16).

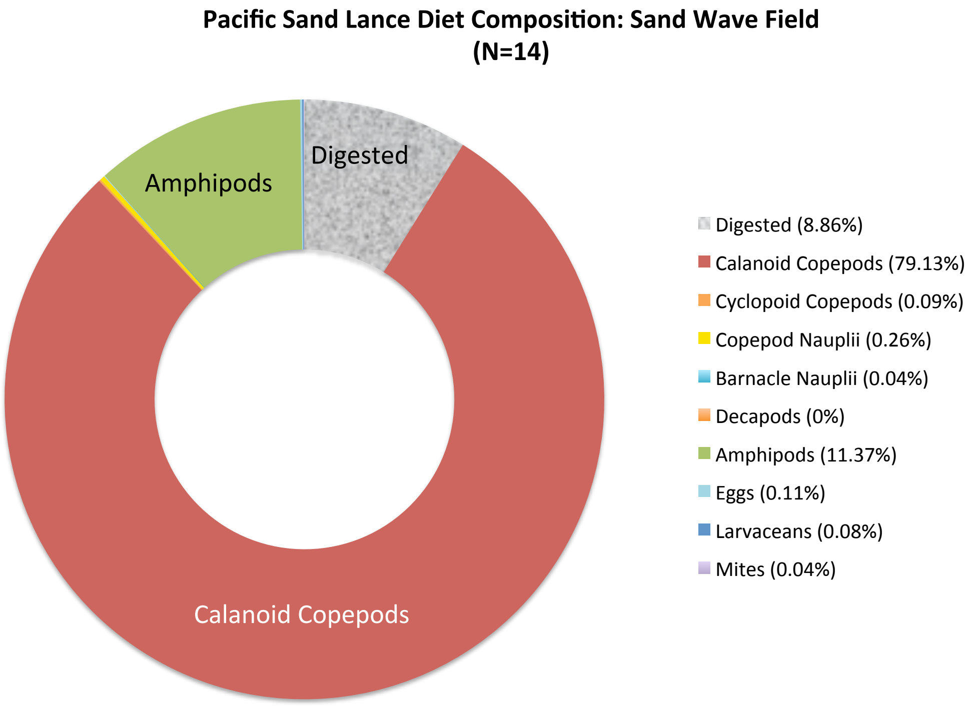
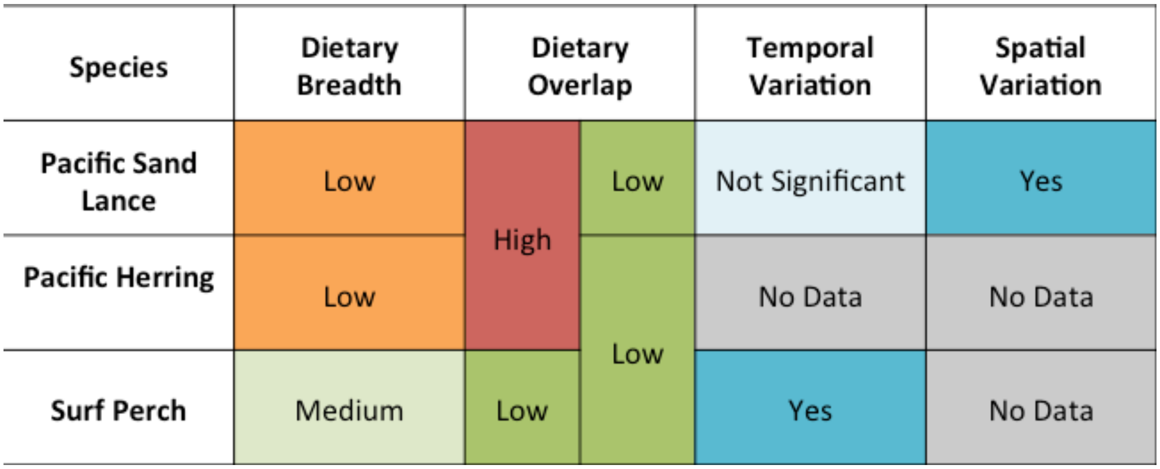


Figure 12. Seasonal average of SP diet composition at sand Wave Field (N = 14).

II. Tables

Table 1: Summary table of analyses conducted and their results.



Species	Dietary Breadth	Dietary Overlap		Temporal Variation	Spatial Variation
Pacific Sand Lance	Low	High	Low	Not Significant	Yes
Pacific Herring	Low		Low	No Data	No Data
Surf Perch	Medium	Low		Yes	No Data