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Feeding Ecology of the Pacific Sand Lance (*Ammodytes hexapterus*): Understanding the Trophic Role of an Important Forage Fish in the San Juan Archipelago

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Abstract- Forage fish such as herring, surf perch and Pacific sand lance are a crucial link between lower and upper elements in the food chain, transferring dense energy and vitamin content from primary producers (phytoplankton) to higher trophic levels (piscivorous fishes, birds, and marine mammals). In this study we examined the feeding ecology and trophic role of *A. hexapterus* in the San Juan Archipelago. We collected data on mass, fork length, population structure, substrate, and stomach contents and used a chi-square test to examine whether or not there were differences in fullness and digestion as a function diel, tidal and seasonal cycles. Our results suggest that time of day has a significant influence on stomach fullness (X^2 =16.01, P=0.042), but not digestion. Date also significantly drives patterns in stomach fullness (X^2 =60.57, P=0.019), but not in digestion. We used a generalized linear model to account for the corresponding effects of tidal, diel, and seasonal trends as well as difference in habitat affinity for different substrates in driving patterns of catch per unit effort (CPUE). CPUE was significantly different across the course of the fall (F_1= 3.00, p=0.093) and in different substrate types (F_1= 12.49, p=0.001). This study can be used to inform fisheries managers and add higher resolution to food web models.

Keywords. — Pacific Sand Lance; *Ammodytes hexapterus;* San Juan Archipelago; Feeding ecology; Catch Per Unit Effort; Trophic levels.

INTRODUCTION

The efficient transfer of energy between primary and higher trophic levels in a marine ecosystem falls on a few species of highly abundant, small forage fish. This type of community structure, known as a “wasp-waist ecosystem,” is characterized by abundant diversity at the bottom and top of the food web with fewer species present at the intermediate levels (Curry et al. 2000). Forage fish are a crucial link between lower and upper elements in the food chain, transferring dense energy and vitamin content from primary producers (phytoplankton) to higher trophic levels (piscivorous fishes, birds, and marine mammals) (Robards et al. 1999). These fish also act as channels of mass and energy flow between different habitats; many forage fish species occupy intertidal and sub tidal communities (Emmett et al. 1991). Thus, planktivorous fishes are an important component in driving trophic dynamics in many ecosystems. Disruptions and variations in the abundance of forage fish populations can significantly impact marine ecosystems (Bargmann 1998).

The marine ecosystem of the Salish Sea and the San Juan Channel support large populations of forage fish as well as important commercial fisheries which exploit them. All but Pacific sand lance *(Ammodytes hexapterus)* are commercially fished in the state of Washington. Yet these fish are thought to be of great ecological importance to local marine food webs. (Bargmann 1998, Gillman 1994). They are a known food source for 29 species of birds, 10 species of marine mammals, and 30 species of commercial and sport fishes (Meyer et al. 1979). Population declines in *A. hexapterus* have contributed to large scale breeding failure among various seabird species (Haynes, Ronconi, & Burger, 2007).

A. hexapterus are typically found in nearshore areas with coarse sand substrate. Foraging is believed to take place in the early morning and evening but it is also thought the species forage while schooling in the middle of the day (Hobson 1986; Blaine 2006; Clayman 2001; Robards et al. 1999). During the spring, summer and early fall months, *A. hexapterus* is considered epibenthic; they are thought to school pelagically during the day and burrow in substrate at night to conserve energy and avoid predation (Greene 2011; Haynes 2007; Field 1988; Robards 1999). Conversely in the winter months, the species enters a state of hibernation, remaining buried in the sediment for prolonged periods of time (Fives et al. 1967; Robards et al. 1999).

Though many endangered species in the San Juan area, such as chinook salmon, rely on *A. hexapterus*, surprisingly little research has been published on the feeding ecology of this population. Therefore, the purpose of this experiment is to (1) quantify the diet preferences of *A. hexapterus*, (2) determine their feeding characteristics, including the effect of tide, diel and seasonal cycles, and the correlation between size and predation patterns, and (3) estimate their abundance in the San Juan Channel to calculate top-down control of zooplankton. Due to the importance of this fish, determining the feeding ecology of an important mid-trophic level species is critical to the assessment of ecosystem-level effects on species composition and diversity, thereby providing a better understanding of the ecosystem of Salish Sea as a whole (Bizzarro et al. 2007).

METHODS

Study Site

The San Juan Channel is the focus of a long term monitoring study undertaken by the University of Washington. The 21.5km long transect begins at the North station which is located between San Juan and Orcas Islands (48º35.00’ N, 123º02.50’ W) and ends at the South station which is located south of the mouth of Cattle Pass, in the Strait of Juan de Fuca (48º25.20’ N, 122º56.60’ W). The San Juan Channel sand wave field runs north (48º31.333’ N, 122º57.083’ W) to south (48º30.333’ N, 122º57.167’ W) and is located between San Juan Island and Lopez Island in the bottom third of the San Juan Channel. The sand wave is primarily comprised of non-uniform sediment depositions of sand, gravel and shell hash and covers an area ~ 531,893m^2 at depths of 60-80 m (Blaine 2006; Greene 2011).

Van Veen Sediment Grabs

A. hexapterus were sampled using a Van Veen grab sampler, a clamshell type sampler that allows samples to be taken from unconsolidated sediment using tension to trap sediment and fish. The Van Veen collected a 0.12m^2 sample per drop and its weight allows for vertical descents even in areas with strong currents and tidal flow. Random samples were taken during eight cruises on the University of Washington’s R/V *Centennial*, between September 28th and November 14th with a total of 43 successful grabs. During each cruise random samples were taken from two locations on the North end of the sand wave, two locations in the central part and two locations on the South end of the sand wave. Supplementary samples to fill in gaps in diel and tidal cycles were taken on the R/V *Auklet*; October 21st, 2012 (3 samples), November 1st, 2012 (3), November 8th, 2012 (2). Grabs were counted if the Van Veen successfully sealed and remained closed to retain sediment (e.g. did not latch onto large gravel of rocks, preventing closure). The contents of each Van Veen grab was transferred into a large plastic bin, where the sediment was combed through twice to ensure all sand lance had been found. Fish were placed in sampling bottles filled with seawater and euthanized with a lethal dose of tricaine methanesulfonate (MS-222) and fixed with 30mL of buffered formalin (formaldehyde supersaturated with Borax) to preserve the sample.

Mass, Fork Length & Population Structure

Mass and fork length were taken for each individual fish. Mass was measured to the nearest 0.01g using an OHAUS Scout Pro 400g x 0.01g scale. Fork length was taken to avoid discrepancies in the fraying of the tail and was measured to the nearest whole mm. For all individuals, age class was determined based on fork length. Age-at-length metrics were determined by Tina Wylie-Echeverria (2010, unpublished data) where fish under 69mm were young of year (age 0), fish between 70-109mm were age 1, fish between 110-129mm were age 2, and fish between 130-150mm were age 3.

Stomach Content Analysis

Grab samples taken on the same day were grouped together based on geographic location on the sand wave. From each sample, five fish from each age class were randomly selected for stomach content analysis. Using a scalpel, fish were cut anteriorly along the left lateral axis beginning at the anal opening and ending at the operculum. Internal organs were removed and placed in a petri dish, while the stomach was removed separately. Stomach fullness was assessed prior to excising the contents using a rank 0 (empty) - 4 (distended). Using a pair of forceps to grasp the stomach, the contents were excised using a dissecting pin and the digestion state was given a rank 0 (not digested) - 4 (too digested to identify). Stomach contents were counted using a dissecting scope (Nikon SMZ645) and laboratory counters. Each individual organism was identified to lowest taxonomic class possible. Analysis was done using frequency occurrence and numerical methods by Hyslop (1980). In the frequency of occurrence method, food items was expressed as the percentage of the total number of stomach containing food. In the numerical method the number of each food item was expressed as the percentage of the total number of food items found in the stomachs as well as the mean number of individuals per stomach in each food category (Oso, Ayodele, & Fagbuaro, 2006).

Catch per Unit Effort and Abundance

Catch per Unit Effort (CPUE) was used to assess the abundance of *A. hexapterus*. CPUE was estimated using the equation:

$$\frac{Total\ number\ of\ fish}{Total\ number\ of\ succesful\ grabs}$$

Abundance was estimated using the equation (.12m^2 represents the area of the Van Veen and 531,893m^2 represents the area of the sand wave):

$$\frac{CPUE}{0.12\mathrm{m}^2} * 531{,}893m^2$$

Feeding Pressure

Feeding pressure was calculated using a density estimate calculated with the equation:

$$\frac{24\ fish}{.22m * .45m * .26m} = fish/m^3$$

where 24 fish is the season CPUE, .22m is the height of the Van Veen grab, .45m is the length of the Van Veen grab and .26m is the width of the Van Veen grab. To estimate feeding pressure the following equation was used:

$$density\ of\ fish * .030g = grams\ of\ biomass$$

where .030g is the average weight of all the full stomachs.

Zooplankton Sampling

Zooplankton samples were collected on seven of the eight (no sample collected on October 25th, 2012) Van Veen sampling cruises aboard the R/V *Centennial* at two stations in the San Juan Channel. The samples were collected by vertical tows using a 70cm diameter, 153µm mesh net weighted at the cod end. The net was lowered to a depth of 10m above the channel bottom. All tows were assumed to have sampled a cylindrical mass of water, the volume of which was calculated with the equation:

$$V = \pi(0.35)^2 * l$$

where V is the tow volume in m^3, 0.35 is the radius of the net mouth in m, and l is the length in meters of cable from the surface to the net's mouth.

In the lab, each sample was filtered with a 118µm mesh. The plankton were re-suspended in fresh water and split to ½ or ¼ dilution, depending on perceived density. Each split was diluted to 700mL for counting. Two aliquots of 5mL each were taken from each tow using a Stempel pipette and placed in a petri dish. Individuals were counted to the lowest taxonomic class using a Nikon SMZ645 dissecting scope and laboratory counters. Total densities were calculated using the equation:

$$D = \frac{(N * 700\mathrm{mL})/(d * a)}{V}$$

where *D* is the density of organisms in individuals/m^3, *N* is the total count of organisms counted in the aliquot sample, 700mL is the volume of the split sample, *d* is the dilution of the split as a fraction of 1, *a* is the volume in mL of the aliquot counted, and *V* is the total volume of water sampled by the tow net, as calculated above. No plankton tows were conducted directly over the sand wave so zooplankton densities from the North and South station were averaged per cruise.

Statistical Analysis

Sigma Plot® 11.0 was used to conduct a linear regression of cruise date and CPUE. R 2.15 was used to run a Chi-Squared test to describe relationships between our dependent variables: time of day and tide to our response variable (stomach fullness and digestive state). Microsoft® Excel 2011 was used to calculate percent number and percent frequency.

RESULTS

A total of 1,032 specimens of *Ammodytes hexapterus* were obtained and 155 specimens were used for stomach contents analysis. The standard length ranged from 23.0-137.0 mm, while the weight ranged from 0.61-16.0 g.

Stomach Contents

In September, Calanoid copepods accounted for 75.0% of the content under frequency of occurrence method followed by Amphipods with 50.0% and unidentified copepods with 25.0% (Table 1). In the numerical pooled analysis, Calanoid copepods comprised 97.14% of the diet, followed by Amphipods (1.9%) and unidentified copepods (0.95%). Using the numerical individual analysis method, Calanoid copepods constituted 73.31% of the organisms in a stomach, while unidentified copepods and Amphipods represented 25.0% and 1.68% respectively. Out of 13 stomachs examined, nine (69.23%) had empty stomachs in the month of September (Table 2).

In October, unidentified organisms accounted for 68.0% of the content under frequency of occurrence method followed by unidentified copepods with 64.0% while Polychaete worms were the least observed (4.0%) (Table 3). In the numerical pooled analysis, unidentified copepods were the main part of the diet (50.03%), followed by Cocinodiscus (21.35%), while Polychaete worms were the least (0.26%) important. Using the numerical individual analysis method, unidentified copepods comprised 48.01% of the organisms in a stomach, followed by unidentified organisms (34.81%). Polychaete worms (0.01%) represented the fewest organisms found in a stomach. Out of 85 stomachs examined, 60 (70.58%) had empty stomachs in the month of October (Table 2).

Under the frequency of occurrence method all organisms represented 50% of the stomach contents in November (Table 4). In the numerical pooled analysis, unidentified copepods constituted 41.17% of the diet, followed by Calanoid copepods (16.47%) and Cocinodiscus (14.11%). Using the numerical individual analysis method, unidentified organisms and unidentified copepods constituted 50.0% and 22.15% respectively of the organisms in a stomach, while Polychaete worms (0.63%) represented the fewest organisms found in a stomach. Out of 57 stomachs examined, 55 (96.49%) had empty stomachs in the month of November (Table 2).

Feeding Pressure

Using the season CPUE (24 fish) and the volume of the Van Veen (.026 m^3), the total average density of *A. hexapterus* in the sand wave was 13 fish/m^3. Given the mean weight of all full stomachs (stomach fullness: 4, weight: 0.03g), it is estimated that *A. hexapterus* are capable of consuming .40 g of biomass until satiated. Comparatively the mean density of organisms per sampling cruise was 2245 organisms/ m^3 of water.

Fullness and Digestion

Mean stomach fullness by time of day has a significant influence on stomach fullness (X^2 =16.01, *P*=0.042), but not digestion (X^2 = 5.01, *P*= 0.542). Patterns in stomach fullness are influenced by date (X^2 =60.57, *P*=0.019), but not digestion (X^2 =44.26, *P*=0.045). Tidal cycles showed a definite trend but were not significant for either fullness (X^2 =17.17, *P*=0.375) or digestion (X^2 =4.30, *P*=0.828). The mean stomach fullness and digestive state by age were both highest for Age 0 (F=0.69, D=0.97) and lowest for Age 3 (F=0, D=0) (Table 5). There is a significant relationship between fullness and digestion (X^2=19.56, P=0.003)

Catch per Unit Effort

A total of 1,032 fish were sampled from the eight cruises; with a total of 43 Van Veen grabs in the San Juan Channel sand wave field. This resulted in a mean Catch per Unit Effort

(CPUE) of 24 fish. There was a significant difference in CPUE between sampling date (R^2=0.51, p=0.017) (Fig. 1). Additionally, CPUE was significantly different across the course of the fall (F_1= 3.00, p=0.093) (Fig. 2). The mean CPUE across time of day showed an upward trend as the day progressed but was not significant (F_1= 0.16, p=0.683) (Fig. 3). The mean CPUE across locations was highest in the center of the sand wave where the bottom type was predominantly sand (North: 14, Center: 32, South: 26) (Fig. 4), furthermore sediment type was found to significantly affect CPUE (F_1= 12.49, p=0.001). The mean CPUE across the tidal cycle showed a definite trend but was not statistically significant (F_1= 0.34, p=0.880) (Fig. 5).

Population Estimate

Based on the season CPUE (24 fish), the surface area of the Van Veen (0.12 m^2), and the area of the sand wave field (531,893 m^2) it is estimated there are 106,378,600 *A. hexapterus* in the San Juan Channel sand wave field.

DISCUSSION

Trends Over Time

The scale of this study provides a new perspective on the interacting effects of tidal, diel, and seasonal trends as well as difference in habitat affinity for different substrates in driving patterns of CPUE. Over the course of the Fall 2012 season in the San Juan Channel sand wave field, CPUE had a significant trend as the season moved towards winter. During sampling efforts in the month of September, mean CPUE was 18.5, where November mean CPUE was 30.27. Coupled with higher abundance, stomach fullness was significantly impacted by monthly shifts while digestive rates also had a downward trend. A general decrease in stomach fullness and digestive state was observed as the season progressed. The increase in *A. hexapterus* abundance in the sand wave associated with lower stomach fullness and digestive state are suggestive of *A. hexapterus* moving into a state of winter dormancy, beginning in late-October. Studies have observed similar occurrences; Robards, M. D., Piatt, J. F., Wilson, M. F., Armstrong (1999) and noted that sand lance are rarely caught in the water column during winter months, furthermore Ciannelli (1996) found prolonged gut evacuation times for hibernating sand lance. Food remained in the stomach for as long as 30 hours during winter months, suggesting a digestion time of 45-80 hours (Ciannelli, 1996).

Daily movement of *A. hexapterus* suggests crepuscular behavior between benthic substrate and the pelagic water column. These vertical movements are tied to feeding and predation avoidance, suggesting daily schooling and burrowing behavior during diel cycles (Hobson, 1986; Robards, M. D., 1999). Sampling results showed CPUE lowest during the morning and increasing throughout the day, furthermore results suggest that time of day has a significant influence on stomach fullness but not digestion. Stomach fullness and digestion were found to be highest in the morning and evening. Our results depict feeding behavior occurring in the morning and evening with minimal digestion occurring during those times with burrowing behavior occurring during the afternoon and night.

The effect of tide rips and complex bathymetry on marine mammal, pelagic bird, and planktivorous fish feeding behavior are well documented. Many studies have noted an increase in foraging behavior among many species in areas of high tidal flow (Zamon 2003). Our CPUE results suggest that definite trends exist over the course of the tidal cycle in terms of *A. hexapterus* abundance. Sand lance exhibit stationary schooling behavior when feeding and increase nearest-neighbor distances when they feed on plankton (Robards et al. 1999). Copepods, the primary source of prey for sand lance are significantly more abundant in the southern region of the San Juan Channel during flood tides than during ebb tides (Sigley, pers. comm, Zamon, 2003). CPUE results show highest abundances in the sand wave during high floods and decreasing towards slack tides and ebbing tides. These results suggest sand lance are feeding during times of slower moving water, possibly due to morphological make-up as well as increased predation risk during high tide rips (Zamon, 2003). However, an association remains between flooding tidal currents, increased copepod abundance and sand lance abundance. Similar behavior has been described in Alaska (Hobson, 1986; Zamon, 2003). By looking at stomach fullness and digestive state over the course of a tidal cycle, the fullest stomachs and highest state of digestion occur during fast ebb tides and decrease as the tidal cycle moves to flooding tides. Previous studies have reported the feeding response of planktivorous fishes to changing currents, however very few have looked exclusively at non-reef species. Our results suggest that feeding trends of sand lance stomach fullness and digestive state were consistent with daytime feeding on plankton and changing currents (Zamon, 2003).

The major food items found in *A. hexapterus* sampled in the San Juan Channel sand wave field were consistent with plankton tow data throughout Fall 2012 suggesting that *A. hexapterus* are opportunistic generalist feeders. In the month of September, Calanoid copepods dominated the diet of *A. hexapterus*, while in October unidentified copepods and Cocinodiscus were most present and in November stomachs contained mostly unidentified copepods. Overall, Arthropoda species dominated the diets, which is consistent with prior studies (Robards et al. 1999). The presence of Cocinodiscus is notable as they were present in one-year-old fish. Though the feeding occurrence was slight among the sampled fish (n=2), predation upon a phytoplankton species suggests that *A. hexapterus* discern their prey. Studies have shown that vision is far more important than olfaction in feeding for *A. hexapterus* (Robards et al. 1999). The presence of phytoplankton also indicates that *A. hexapterus* are preying on both primary producers and primary consumers thus altering the flow of energy available through the different trophic levels.

A. hexapterus represent an important part of the food web in Puget Sound, however no biomass data exists for the species. Forage fish, including sand lance, surf smelt and herring are key components in the energy transfer between primary producers and primary consumers upwards to piscivorous fish such as salmon and pelagic predators such as marine mammals and pelagic birds. In the San Juan Channel, *A. hexapterus* are especially important in structuring near shore marine predator–prey interactions and food web dynamics (Zamon, 2003). Through our CPUE results, we were able to estimate the feeding pressure of *A. hexapterus* on the plankton community. *A. hexapterus* are capable of consuming 0.40 g of biomass until satiated; this figure is a vital step in understanding ecosystem and food web dynamics. Having data on all species in an ecosystem is an important part of food web modeling and gives fisheries managers higher resolution of how the ecosystem functions as a whole. Continuous refinement of this biomass figure is an important step to ensure the stable existence of the Puget Sound ecosystem (Harvey et al. 2010).

Future Study Efforts

Incorporating seasonal surveying of the San Juan Channel sand wave would help us understand how *A. hexapterus* adapt to seasonal changes and broaden the results and conclusions of our study. Additionally, implementing finer scale sampling over tidal and diel cycles as well as increasing the precision of our methods will help us better understand and predict the feeding characteristics of *A. hexapterus*. Considering other sand waves will increase our understanding of what habitat types are most preferred as well as give us a better estimate of *A. hexapterus* in the San Juan Archipelago.

Acknowledgments

I would like to thank Matt Baker, Jan Newton, Breck Tyler and Ryan McLaughlin for their assistance and continued support. I would also like to thank Adam Summers and Joe Bizzarro at the University of Washington Friday Harbor Laboratories for their professional expertise. I also thank Gary Greene and John Aschoff for the use of geographic images of the sand wave and geospatial analysis assistance. A special thanks to Captain Dennis Willows and Wolf Krieger of the *R/V Centennial* and all my Pelagic Ecosystem Function colleagues, the marine biology students and the Friday Harbor Lab community for their assistance throughout the course of this study.

Literature Cited

Bizzarro, J. J., Robinson, H. J., Rinewalt, C. S., & Ebert, D. a. (2007). Comparative feeding ecology of four sympatric skate species off central California, USA. *Environmental Biology of Fishes*, *80*(2-3), 197–220.

Ciannelli, L. (1996). *Winter Dormancy in the Pacific Sand Lance (Ammodytes hexapterus) in Relation to Gut Evacuation Time* (pp. 95–105).

Haynes, T. B., Ronconi, R. A., & Burger, A. E. (2007). Habitat Use And Behavior Of The Pacific Sand Lance (Ammodytes Hexapterus) In The Shallow Subtidal Region Of Southwestern Vancouver Island (Ammodytes Hexapterus) In The Shallow Subtidal. *Northwest Naturalist*, *88*(3), 155–167.

Hobson, S. E. (1986). Predation on the Pacific Sand Lance , Ammodytes hexapterus (Pisces : Ammodytidae), during the Transition between Day and Night in Southeastern Alaska. *Copeia*, *1986*(1), 223–226.

Emmett, R.L., S.L. Stone, S.A. Hinton, and M.E. Monaco. 1991. Distribution and Abundance of 21 Fishes and Invertebrates in West Coast Estuaries, Volume II: Species Life History Summaries. Rockville, Maryland: NOAA/NOA Strategic Environmental Assessments Division.

Field, L.J. 1988. Pacific sand lance, Ammodytes hexapterus, with notes on related Ammodytes species. In: Wilimovsky, N.J.; Incze, L.S.; Westrheim, S.J., eds. Species synopses, life histories of selected fish and shellfish of the northeast Pacific and Bering Sea. 15-33. Available from: Washington Sea Grant Program, 3716 Brooklyn Ave. NE, Seattle, WA 98105.

Fives, J.M. 1967. Sandeels Ammodytes and their larvae off the Galway coast. Scientific Proceedings of the Royal Dublin Society, Series B. 2(4): 37-44.

Harvey, C.J., K.K. Bartz, J. Davies, T.B. Francis, T.P. Good, A.D. Guerry, B. Hanson, K.K. Holsman, J. Miller, M.L. Plummer, J.C.P. Reum, L.D. Rhodes, C.A. Rice, J.F. Samhouri, G.D. Williams, N. Yoder, P.S. Levin, and M.H. Ruckelshaus. 2010. A mass-balance model for evaluating food web structure and community-scale indicators in the central basin of Puget Sound. U.S. Dept. Commer., NOAA Tech. Memo. NMFS NWFSC-106, 180 p.

Hobson, S. E. (1986). Predation on the Pacific Sand Lance , Ammodytes hexapterus (Pisces: Ammodytidae), during the Transition between Day and Night in Southeastern Alaska. *Copeia*, *1986*(1), 223–226.

Hyslop, E. J. (1980). Stomach contents analysis-a review of methods and their application. *Journal of Fish Biology*, *17*(4), 411–429.

Oso, J. A., Ayodele, I. A., & Fagbuaro, O. (2006). Food and Feeding Habits of Oreochromis niloticus (L .) and Sarotherodon galilaeus (L .) in a Trophical Reservoir. *World Journal of Zoology*, *1*(2), 118–121.

Robards, M. D., Piatt, J. F., Wilson, M. F., Armstrong, R. H. (1999). *Sand Lance : A Review of Biology and Predator Relations and Annotated Bibliography*.

Zamon, J. (2003). Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Marine Ecology Progress Series*, *261*(1), 243–255.

Table 1: Summary of the stomach contents of *A. hexapterus* in September

Food items	No.	%FO	%N	%N Individual
Arthropoda:				
Amphipod	2	50.0	1.9	1.68
Calanoid Copepod	3	75.0	97.14	73.31
Unidentified Copepod	1	25.0	0.95	25.0

Table 2: Analysis of empty stomachs in A. hexapterus

	No. of stomachs examined	No. of empty stomachs	% of empty stomach
Months			
September	13	9	69.23
October	85	60	70.58
November	57	55	96.49

Table 3: Summary of the stomach contents of *A. hexapterus* in October

Food items	No.	%FO	%N	%N Individual
Arthropoda:				
Amphipod	12	48.0	4.94	4.37
Calanoid Copepod	2	8.0	1.12	0.26
Cyclapoid Copepod	3	12.0	8.17	5.56
Harpacticoid Copepod	4	16.0	1.38	0.62
Unidentified Copepod	16	64.0	50.03	48.01
Bacillariophyta:				
Cocinodiscus	3	12.0	21.35	6.31
Bacillariophyta:				
Polychaete Worm	1	4.0	0.26	0.01
Unidentified Organism	17	68.0	12.72	34.81

Table 4: Summary of the stomach contents of *A. hexapterus* in November

Food items	No.	%FO	%N	%N Individual
Arthropoda:				
Amphipod	1	50.0	7.05	3.79
Calanoid Copepod	1	50.0	16.47	8.86
Cyclapoid Copepod	1	50.0	12.94	6.96
Unidentified Copepod	1	50.0	41.17	22.15
Bacillariophyta:				
Cocinodiscus	1	50.0	14.11	7.59
Bacillariophyta:				
Polychaete Worm	1	50.0	1.17	0.63
Unidentified Organism	1	50.0	7.05	50.0

Table 5. Mean stomach fullness and digestive state by age of fish.

Age 0	**Fullness**	**Digestion**
	0.69047619	0.976190476
Age 1	**Fullness**	**Digestion**
	0.534883721	0.662790698
Age 2	**Fullness**	**Digestion**
	0.32	0.24
Age 3	**Fullness**	**Digestion**
	0	0

Figure 1. Linear Regression of Catch per Unit Effort by Julian date.

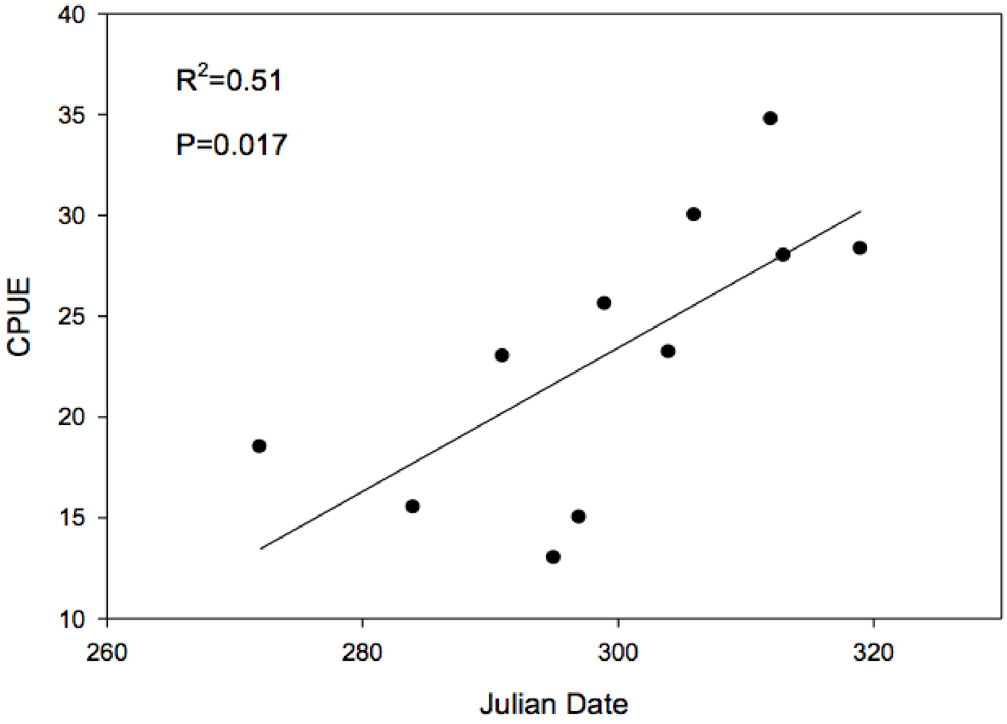

Figure 2. Catch per Unit Effort by Month.

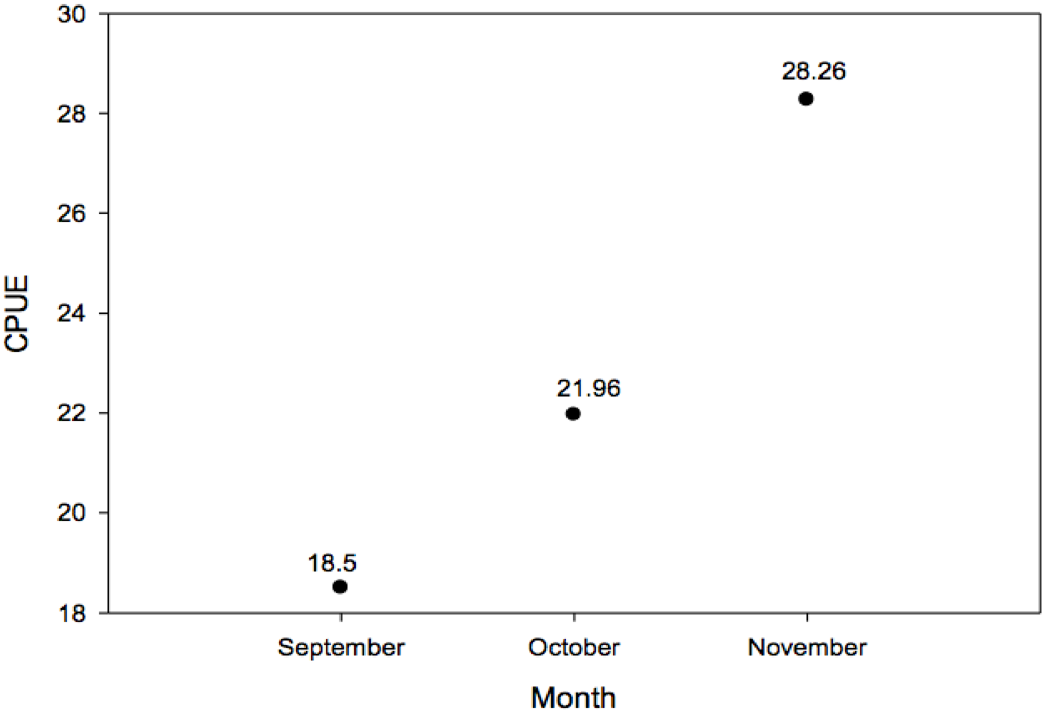

Figure 3. Catch per Unit Effort by Time of Day.

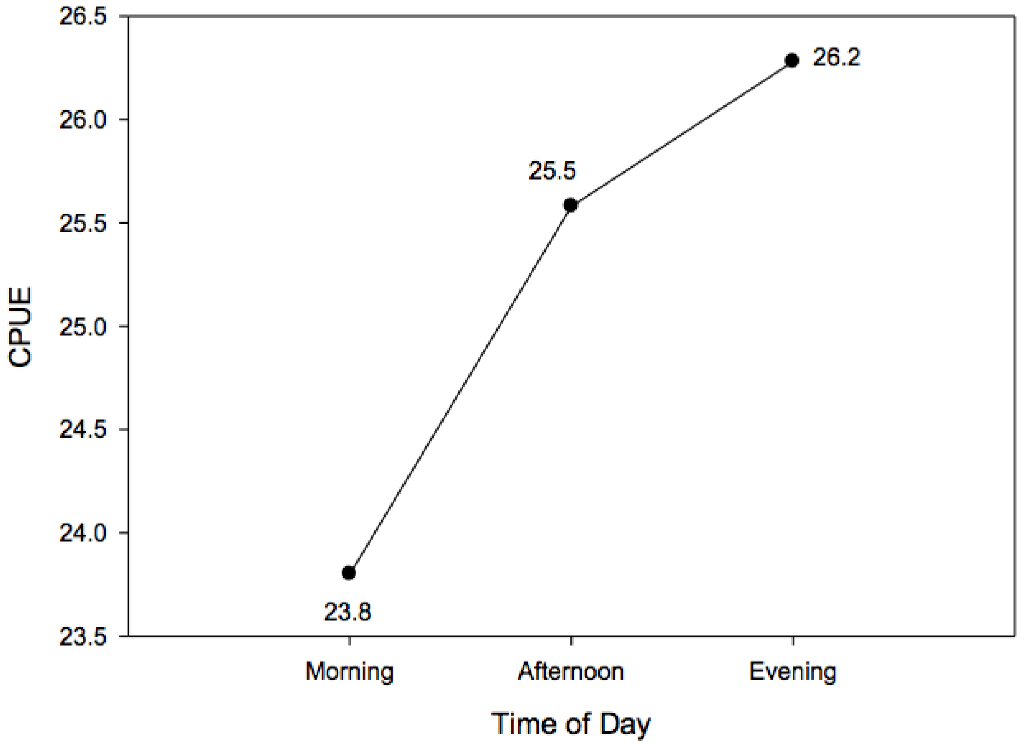

Figure 4. Catch per Unit Effort by Location on sand wave

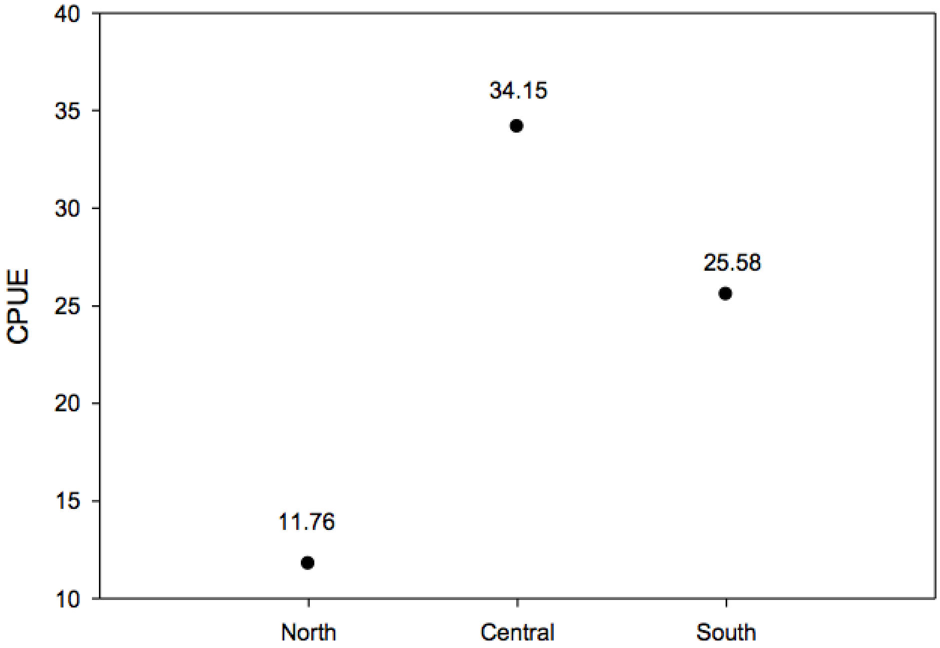

Figure 5. Catch per Unit Effort by Tide Cycle