Examination of the seasonal variation in the abundance of *Crangon* shrimp and its relationship to the presence of the green sturgeon (*Acipenser medirostris*)

Nikolai M. Danilchik, Sarah K. Henkel, David D. Huff

Abstract

A better understanding of the seasonal and spatial distribution of *Crangon* shrimp and their relationship with their predators, including the green sturgeon, *Acipenser medirostris*, is an important step toward the larger goal to understand food webs of the nearshore continental shelf of the northeastern Pacific. Here, I examined how the biomass and energetics of two species of *Crangon* varied seasonally and by depth and the relationship between those patterns and the modeled distribution of *A. medirostris*, hypothesizing that the predicted presence of sturgeon would show a positive relationship with *Crangon*.

Crangon samples were collected via beam trawl near Newport, Oregon, in 15 months over a span of 3 years. The presence of *A. medirostris* was predicted using a model based on data from coastal hydrophone arrays tracking acoustically tagged sturgeon, that included a number of physical covariates.

Subsequent analyses found that for the most part, biomass density of *Crangon* was higher in fall and late summer than in winter or spring, driven by the more abundant *C. alaskensis*. Alternatively, *Crangon stylirostris* was most abundant in February and at shallower depths. Energetics of individual *C. alaskensis* was higher in winter than in fall and at shallower depths, and energetics of *C. stylirostris* showed no effect from month or depth. Biomass density of *Crangon* and calorimetry of *C. alaskensis* were both tested as explanatory

variables for *A. medirostris*, but no relationship was found between these quantities and *A. medirostris* presence.

The observed patterns in *Crangon* abundance and energetics could be explained either by seasonal fluctuation of nutrients caused by upwelling, or by reproductive migration of individual shrimp once they reached sexual maturity. The lack of any correlation between *Crangon* distribution and *A. medirostris* presence doesn't rule out some relationship between the two, but a larger spatial area of *Crangon* sampling might be required to detect those patterns if they exist.

Introduction

Crangon (Fabricius 1798) are a genus of decapod crustaceans in the family *Crangonidae* (Haworth 1825) found in temperate waters of the northern hemisphere in both the Atlantic and the Pacific. On the Oregon coast, they inhabit soft sandy bottoms from estuarine areas to the mid continental shelf. The behavior and ecology of these shrimp are poorly understood and little studied, but they are an important part of estuarine and offshore benthic food webs (Campos et al. 2012). The green sturgeon (*Acipenser medirostris*, Ayres 1854) is an anadromous fish found in the north Pacific ocean. It feeds primarily on benthic organisms, such as clams, crabs, small fish and shrimp - including *Crangon* (Kelly et al. 2006, Israel & Klimley 2008). *A. medirostris* is listed as vulnerable under the IUCN (IUCN 2014) and threatened under the US Endangered Species Act. A thorough understanding of the ecology of these sturgeon and their trophic relationships with other organisms in the continental shelf ecosystem will be invaluable in devising effective conservation strategies for this commercially and ecologically important species (Lindley et al. 2008, Pikitch et al. 2006).

Because the trophic systems of the continental shelf are often structured from the bottom up and are heavily influenced by seasonal fluctuations in primary productivity caused by upwelling, it is reasonable to suspect that as the abundance of an invertebrate genus such as *Crangon* changes, the distribution of its predators will also be affected (Ware et al. 2005). In addition, gaining a better understanding of the habits and ecology of *Crangon* shrimp will fill a significant gap in scientific knowledge about these oft-overlooked but important inhabitants of the shallow coastal northeastern Pacific. This project examines the spatial and temporal variability of *Crangon* abundance and caloric content and the possible relationship between that variability and the distribution of *A. medirostris*. The approach of this research is to first determine what spatial and seasonal variations exist in the abundance and caloric density of *Crangon* shrimp in the near-shore shelf environment of the central Oregon coast. Here, "abundance" is defined as the biomass density of *Crangon* in grams per square meter. Caloric density is the chemical energy of *Crangon*, measured in Joules, per square meter. This will only show patterns different from the biomass density if the average chemical energy per individual *Crangon* is variable over space or time. The main spatial variable I examine here is depth, and the study period covers 15 months over a span of approximately 3 years.

My first question is, do abundance and calorimetry of *Crangon* vary between months? I hypothesized that abundance and calorimetry of *Crangon* will be higher in the summer months than the winter months. The mechanism behind this is that chemical energy in the trophic system is elevated in the summer months due to upwelling, so *Crangon* will be found in greater abundance and energy density when food is more plentiful. A null result would show no difference between any months for either abundance or energetics. My second question is, does calorimetry of *Crangon* vary among months or depths? My hypothesis is that *Crangon* will be more energy dense at deeper depths. This is because it is known that

they travel away from the shore in order to spawn (Jarrin & Shanks 2008), and so gravid females in the form of bigger, more energy dense individuals would be expected further from shore. My third question is, if a pattern exists in *Crangon* abundance or calorimetry, would this same pattern also be apparent in the distribution of *A. medirostris*? I hypothesized that there would be a positive correlation between *Crangon* - either in biomass density or average individual energetics - and the presence of *A. medirostris*. Although causality cannot be determined here, such a correlation would not be inconsistent with the mechanism of attraction to prey by the predatory sturgeon, nor with the effects of a third variable that results in greater abundance of both species. A null result would be reported if no correlation exists between the abundance of *Crangon* and the presence of *A. medirostris.*

Materials and Methods

Field Collections

We sampled *Crangon* spp. as part of the baseline characterization of the benthic communities at the Pacific Marine Energy Center North Energy Test Site (PMEC-NETS) near Newport, Oregon, operated by the Northwest Marine Renewable Energy Center at Oregon State University. Invertebrate samples were trawled from the seabed using a two meter wide beam trawl attached to a net with 3mm cod-end liner at three different transects, each of which included stations at 30, 40, and 50 meter depths - for a total of nine stations per visit (Figure 1). Each tow lasted ten minutes, and due to varying conditions the physical length of the tow differed between individual samplings. Sampling took place three to six times per year (every other month during favorable weather conditions), starting in June 2010 and, for the purposes of this study, ending in August 2013 (Table 1).
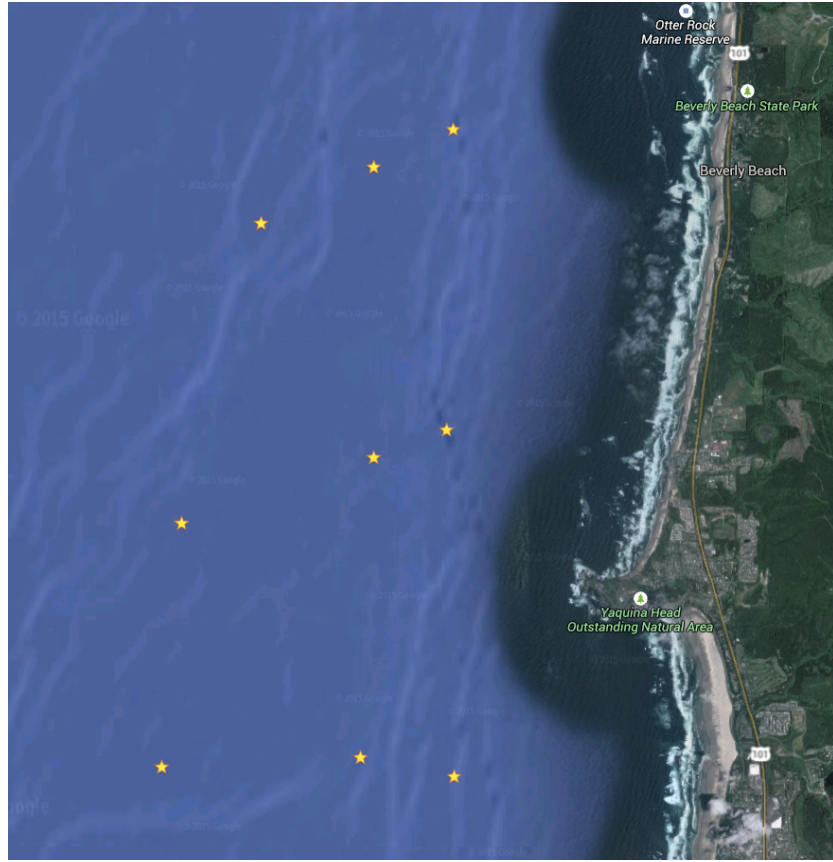
Figure 1: A map of the study area. Markers indicate sampling stations, with trawl depths from left to right at 50, 40, and 30 meters. This map covers a latitude range along the Oregon coast from 44.739967° N to 44.633578° N. (Image: © Google)

Invertebrate samples were flash frozen upon collection and later thawed and then sorted by species. Four *Crangon* species were encountered in the trawl samples, but only two of the species - *C. alaskensis* (Lockington 1877) and *C. stylirostris* (Holmes 1900) - occurred with enough frequency to statistically analyze, so *C. franciscorum* (Stimpson 1856) and *C. alba* (Holmes 1900) were not considered for this study. These latter two species were found sporadically and usually in counts of <20 individuals per sample.

Caloric Analysis

After being sorted to species, the *Crangon* samples were desiccated in a drying oven for 48-72 hours at 65°C, after which they were removed from the oven and dry weighed. In conjunction with the tow area of each trawl, this enabled me to obtain the grams of *Crangon* for both species per square meter trawled.

Table 1: Chart of the years and months in which trawl sampling took place. A "Y" denotes a year and month in which samples were preserved in 70% EtOH prior to desiccation and dry weighing; an "N" means no chemical preservation was used.

	2010	2011	2012	2013
January				
February		Y		
March				
April				N
May		Y		
June	Y	Y	N	N
July				
August	Y	Y		N
September			N	
October	Y	N		
November			N	
December		Y		

Samples from twelve of the cruises had been preserved in 70% ethanol (Table 1), so it became necessary to adjust their recorded dry mass. I determined an average of 33% the mass had been lost due to preservation. This proportion was obtained by dry weighing and measuring 30 individual *C. alaskensis* specimens that had been frozen only, and 30

individuals from the same month that had been thawed and preserved in 70% ethanol for one month. One month was deemed a sufficient length of time because Qureshi et al. (2008) found that shrimp preserved in 70% ethanol had a diminishing rate of mass loss over time, with the majority of dry mass loss occurring within the first 4 weeks of chemical preservation. Comparing the regression lines of the natural logs of length and mass of both groups showed a consistent average loss of 33% mass across all lengths (Figure 2).
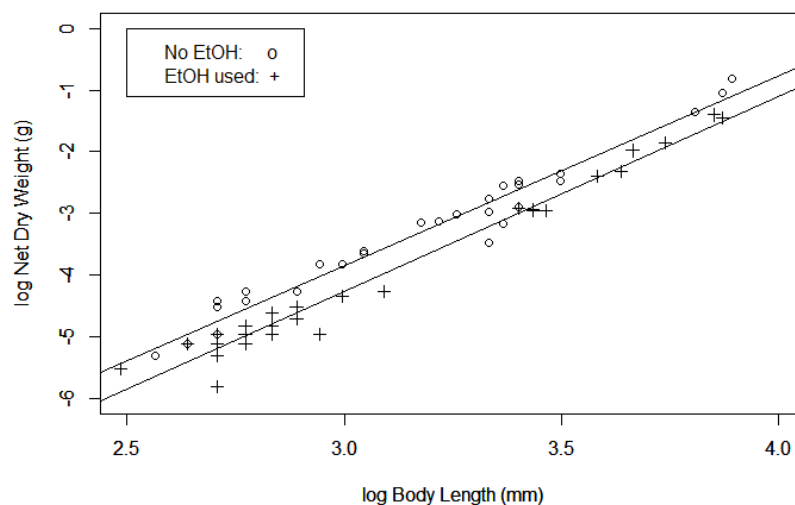
Figure 2: Regressions for the natural log of body length and the natural log of net dry weight of *C. alaskensis*, comparing individuals that were preserved in 70% EtOH with individuals that did not undergo chemical preservation. An average mass loss of 33% was observed for the preserved samples.

After drying, I ground each sample into a fine powder, after which I combusted a sub-sample of approximately 1 gram (when possible) in a Parr model 1341 oxygen bomb calorimeter to obtain a measure of Joules per gram, as per the protocol discussed in the operating instructions for the calorimeter. Deionized water was put in the canister (2000g, ±0.0001g), and the fuse wire used was 10 cm long. Pressure in the combustion chamber was

between 25 and 31 atmospheres, and the masses of samples used were up to approximately

1.20 g, but attempts were made to get each sample as close to 1.00 g as possible.

The energy released by a combusted sample was recorded by observing the rate of

temperature rise of the water in the canister. The formula used to calculate net corrected

temperature rise was as follows (Figure 3):

$$t = t_c - t_a = r_1(b-a) - r_2(c - b)$$

Figure 3: The formula used to calculate net corrected temperature rise of a combusted sample, where t_c is the temperature at time c (the point where temperature stabilized), t_a is the temperature at the time of ignition, a is the time of ignition, b is the time when total temperature rise reaches 60%, c is the time when the temperature stabilized, r_1 is the rate the temperature change before ignition, and r_2 is the rate the temperature changed after time c. (Parr model 1341 operating manual)

To find the gross heat of combustion, the following formula was used (Figure 4):

$$H_g = (t*W - e)/m$$

Figure 4: The formula for gross heat of a sample, H_g. The variable t was determined in the equation in Figure (?), W is the standardized energy equivalent for the calorimeter, e is the heat of combustion of the fuse wire, and m is the mass of the combusted sample. (Parr model 1341 operating manual)

Having acquired the gross heat of a sample in calories per gram, that value was then

converted to Joules by multiplying it by the conversion factor 4.1868. Multiplying Joules per

gram by grams per shrimp for both species and all replicates allowed me to acquire mean

Joules per individual shrimp. The word "caloric" will henceforth be used here to refer to

measurements of energetics in Joules, not actually in calories. I pooled the biomass values

for the two species together into one variable when calculating Joules per square meter, because in that case I am more interested in the total chemical energy available as shrimp, whereas I kept the two species separate for Joules per shrimp, because previous observations showed that *C. alaskensis* is significantly larger on average than *C. stylirostris*. *C. alaskensis* is known to be approximately 0.4 cm longer, on average, than *C. stylirostris* (Lamb & Hanby 2005), and this would be expected to produce a significant difference in average mass between the two species.

Some samples of different stations but the same depth and month had previously been combined in the same jars after determining the mass of shrimp per individual station, but this potential experimental flaw was realized and I subsequently kept each station replicant separate and eliminated those flawed observations from the analyses of Joules per station. For all statistical tests involving Joules, this necessitated the elimination of all data from June 2010 to August 2011, cutting the length of the time series roughly in half, but there were still 9 months of data over a space of 2 years left to analyze. For all statistical analyses involving biomass, the whole data set was still used.

Modeling sturgeon

To determine the probability of presence of *A. medirostris*, a model by Huff et al. (2012) was used. Data for the model were gathered from 2004-2006 and made use of coastal hydrophone tracking arrays that recorded the passage of acoustically-tagged green sturgeon. The study area spanned from the Alaskan coast of the Bering Sea to northern Mexico. Distribution model covariates involved included dissolved oxygen, temperature, depth, north and east currents, and spawning and overwintering attraction (distance to spawning and overwintering grounds). The oceanographic model used biogeochemical

covariates including $Si(OH)_4$, ammonium, nitrate, and silicate, and various plankton and grazers (Huff et al. 2012, Chai et al. 2002). The model was run by Dr. David Huff using depth, latitude/longitude, and date for each data point in the *Crangon* time series, to generate a probability of *A. medirostris* presence.

Statistical Analyses

I first examined biomass density of *Crangon* in relation to space and time with a 3-way ANOVA test of month, depth and year to see if individual months varied among years. Finding months to be consistent across years, I then pooled all years of each month for subsequent analysis. I examined total pooled (of both Crangon species) biomass and the biomass density of each individual species using two-way ANOVA tests with the factors depth and month. I tested average Joules per individual shrimp spatial and temporal variability for both species using two-way ANOVA tests, to find out if shrimp energetics followed the same pattern. Where ANOVA tests indicated significant differences for a factor, I ran a Tukey's Honestly Significant Difference test, which examined the pairwise differences between each combination of months and/or depths. I used total grams per square meter of *Crangon* as an explanatory variable in a linear regression to test whether they had any correlation with sturgeon presence. I repeated this using mean individual Joules of *C. alaskensis* as an explanatory variable.

Results

For total biomass density of *Crangon* (both species combined), October through April had less grams of *Crangon* per square meter than the summer months of May through September (Figure 5a). An ANOVA test with grams of all Crangon per square meter as the

response variable and month and depth as explanatory variables showed that "month" was highly significant in explaining the variation of the response (p<0.001), but depth was not significant (Figure 5b). Tukey's Honestly Significant Difference showed that December (0.012 g/m2) and October (0.015 g/m^2) had significantly less biomass of *Crangon* than August, which had 0.053 g/m^2 (p=0.041, 0.014, resp.) (Figure 5a).
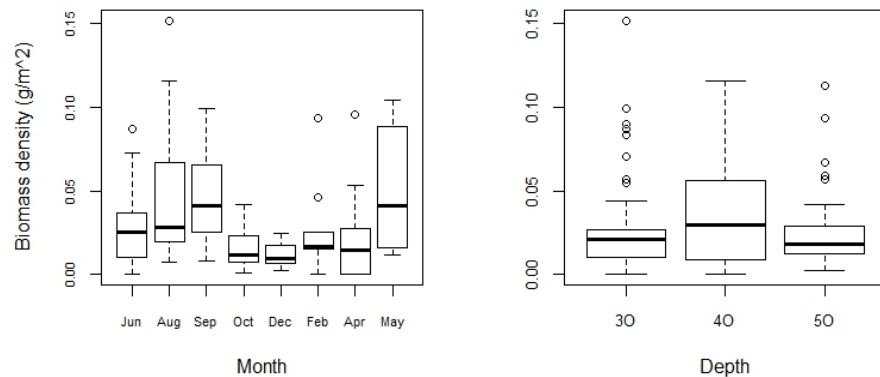

Figure 5: Biomass density of *Crangon* (both species pooled) by month and depth, from June 2010 to August 2013.

For biomass density of *C. alaskensis*, month was again found to be highly significant (p<0.001), and the Tukey test for month in this case showed many pairs of means that were significantly different (Figure 6a; Table 2), but overall the pattern was highest densities in the spring and summer with lower densities in fall and winter. No differences were found with depth (Figure 6b).
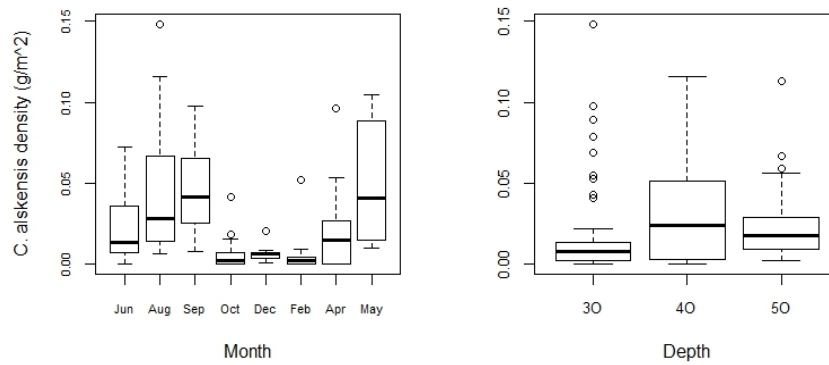
Figure 6: Biomass density of *C. alaskensis* by month and depth, from June 2010 to August 2013.

Table 2: Pairwise comparisons of months for which the difference in biomass density of *C. alaskensis* was significant. The overall trend appears to be a higher biomass in late summer and a lower biomass in winter.

Months	Difference of means (g/m^2)	p value
November-May	-0.044	0.027 *
October-May	-0.042	0.005 **
November-August	-0.038	0.018 *
October-August	-0.037	0.001 ***
December-August	-0.036	0.012 *
February-August	-0.035	0.017 *
September-February	0.040	0.036 *
May-February	0.041	0.030 *
September-December	0.041	0.028 *
September-October	0.041	0.006 **
May-December	0.042	0.023 *
September-November	0.043	0.032 *

An ANOVA test of grams per square meter for *C. stylirostris* showed that depth and month were both significant (p=0.001, <0.001, resp.). The Tukey test for month showed many pairs of months that were significantly different (Table 3). February was found to have a higher mean than September, May, June, December, August, and April (Figure 7a; Table 6).

Table 3: Pairwise comparisons of months for which the difference in biomass density of *C. stiylirostris* was significant.

Months	Difference of means (g/m^2)	p value
February-September	0.019	0.001 ***
February-May	0.018	0.002 **
February-June	0.014	0.002 **
February-December	0.014	0.031 *
February-August	0.017	< 0.001 ***
February-April	0.019	0.001 ***

The Tukey test for depth revealed that the mean biomass density for 30 meters (0.009 g/m^2) was significantly greater than at 40 meters (0.004 g/m^2, p=0.031), and at 50 meters (0.002 g/m^2, p=0.001). The difference between 40 and 50 meters was not significant (Figure 7b).
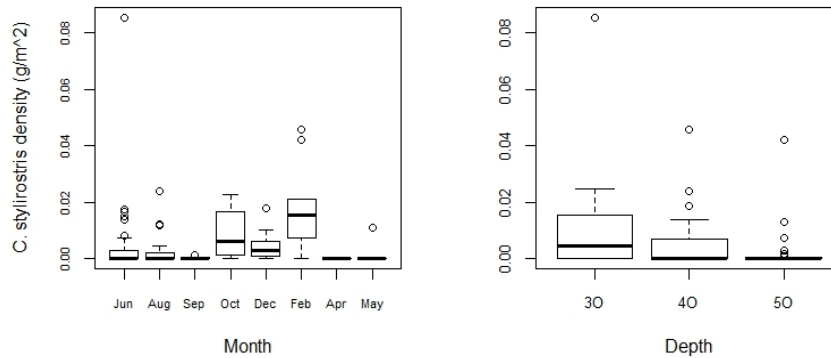
Figure 7: Biomass density of *C. stylirostris* by month and depth, from June 2010 to August 2013.

An ANOVA test of Joules per individual *C. alaskensis* showed significance with both month and depth (p=0.020, 0.024, resp.). The Tukey test for month revealed that the mean for December (4422 J/individ.) was significantly greater than September (865 J/individ., p=0.023) (Figure 8a), and overall trends suggest that caloric content of individuals is higher from fall to spring as compared to summer months, although a great deal of variability was observed. The Tukey test for depth indicated that the mean for 30 meters depth (3745 J/individ.) was significantly greater than for 50 meters (1359 J/individ., p=0.019) (Figure 8b).
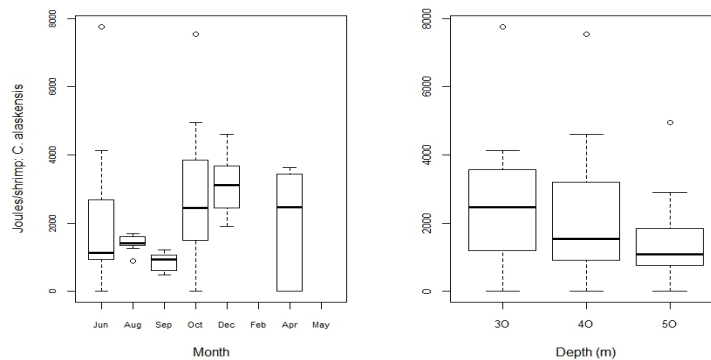

Figure 8: Mean Joules per individual *C. alaskensis* by month and depth, from August 2011 to August 2013.

Mean Joules of individual *C. stylirostris* showed no significant effect from month or depth (Figure 9).
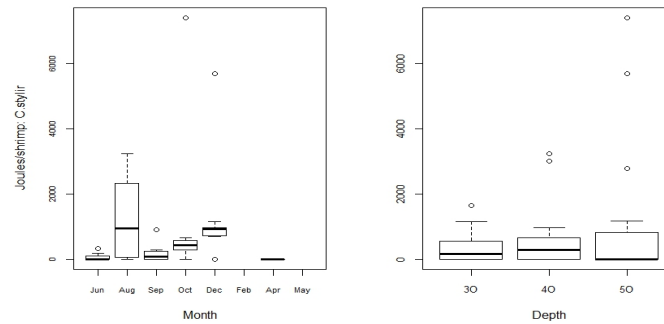

Figure 9: Mean Joules per individual *C. stylirostris* by month and depth, from August 2011 to August 2013.

Having found significant variability in seasonal distribution patterns in both the biomass density of *Crangon* and in the mean individual calorimetry for *C. stylirostris*, I ran linear models with both of those measurements as explanatory variables and modeled *A. medirostris* presence as the response. No correlation was detected with either test (Figure 10), in spite of the fact that *A. medirostris* showed elevated presence in summer and early fall, and at 30 meters depth (Figure 11).
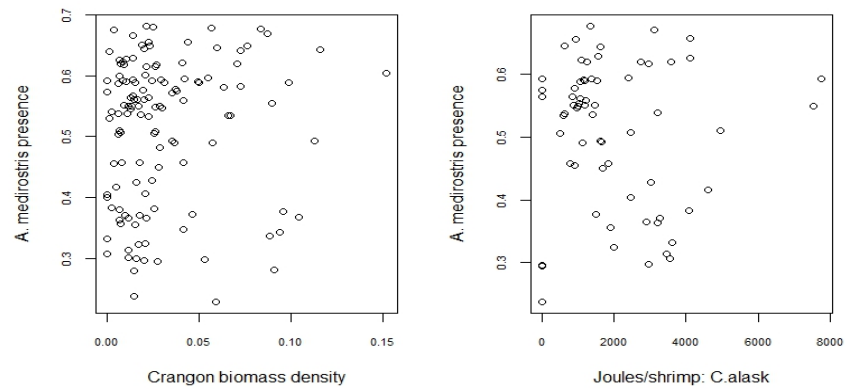
Figure 10: Modeled probability of *A. medirostris* presence compared with *Crangon* biomass density and mean individual Joules of *C. alaskensis*
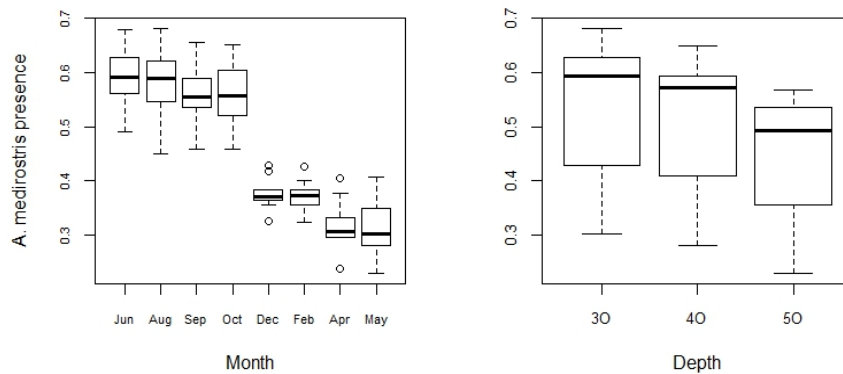

Figure 11: Modeled probability of *A. medirostris* presence, by month and depth.

To summarize, *Crangon* showed a tendency to have higher caloric and biomass density in late summer - especially August - than in the fall and winter months. The exception to this general pattern was biomass density of *C. stylirostris*, which appeared consistently higher in February than other months. *C. alaskensis* appeared to have higher mean individual calorimetry in December than September, and higher at 30 meters depth than at 50 meters.

Discussion

My first hypothesis - that *Crangon* biomass density and mean Joules per shrimp would be greater in summer than winter - was partially supported, because overall biomass density showed a sharp decline after August, and biomass density of *C. alaskensis* followed this pattern even more starkly. The higher biomass density in late summer is consistent with known nutrient cycles in the region, driven primarily by seasonal upwelling of cold, nutrient rich water from the deep sea, which triggers primary productivity in the form of photosynthesis and thus greatly increases available chemical energy in the system through the summer in the form of greater food abundance (Whitney et al. 2005; Varela & Harrison 1999; Small & Menzies 1981). After that point, energy in the system and by extension, available food, drops as expected due to winter current patterns returning and the upwelling diminishing. However, it has been suggested - at least in the case if *C. stylirostris* - that mature adults migrate out onto the continental shelf to spawn in summer and fall, and move back to the shorelines and estuaries in the spring (Jarrin & Shanks 2008). While food availability having a causal effect on abundance of *Crangon* cannot be ruled out, neither can deliberate migration for reproductive purposes.

C. stylirostris did not follow the same pattern as *C. alaskensis*; its biomass density appeared higher in late fall and in winter, with February having a significantly higher mean than many other months. That total biomass density follows the pattern of *C. alaskensis* more closely than *C. stylirostris* should not be surprising, as *C. alaskensis* accounted for the majority of all *Crangon* found in the trawls. The observation of February having a higher mean of *C. stylirostris* should be approached cautiously since February was only sampled once during the entire time series; however, a qualitative look at preceding months (October and December), while not significant, suggests the possibility of biomass of *C. stylirostris*

actually being higher in late fall and winter. An offset distribution pattern between the two species is consistent with the theory of resource partitioning: species that occupy similar niches will tend to partition themselves either spatially or temporally, in order to avoid competing for the same resources (Cartes 1998). This is an inverse distribution pattern similar to that observed in the same area by Givens (2012), in which two species of mysid (*Pacificanthomysis nephrophthalma* and *Archaeomysis grebnitzkii*) had more gravid females present in May (and thus were probably sampled near to their peak annual spawning time), while mysids in the *Neomysis* genus had more gravid females present in October and February. Thus, while abundance of *C. alaskensis* may follow seasonal upwelling patterns, *C. stylirostris* may avoid spawning or migrating onto the shelf until *C. alaskensis* have already mostly left the area. It is also possible that *C. stylirostris* are predominantly concentrated at a depth and time of year not sampled here.

Mean individual energetics of *C. alaskensis* seemed to conflict with my hypothesis. It appeared generally higher in winter and spring rather than summer, with the mean of December being significantly higher than the mean for September. In the context of the pattern followed by biomass density, this indicates that biomass density and mean individual energetics of *C. alaskensis* were inversely related. During the period of the study, total abundance increased through summer, and then rapidly declined after August, at which point mean Joules per individual increased significantly. The implication is that large numbers of less energetic shrimp either die or depart, leaving fewer, more energetic shrimp behind.

My second hypothesis - that *Crangon* would be more abundant and have higher calorimetry values at 50 meters depth than at 30 meters - was not supported, and indeed, was directly contradicted by biomass density of *C. stylirostris* and calorimetry of *C. alaskensis*, both of which were significantly greater at 30 meters than the other depths. In the case of *C.*

alaskensis, it is possible that the proposed mechanism was flawed and should actually work in reverse: instead of producing a result where gravid females (individuals predicted to have higher than average energy density) are found further from shore because they move away from shore to spawn, the same mechanism could instead predict higher energy density nearer to shore because the mature females spawn shortly after leaving bays and estuaries, and then return to the shallows or die without traveling any further out onto the shelf. The higher calorimetry at 30 meters depth detected would then represent the edge of that migration as it moves outward from shore, and the lower energy density elsewhere on the shelf could represent a broader distribution of smaller, sexually immature *Crangon*. Biomass density of *C. stylirostris* being higher at 30 meters depth could also be explained by the same modified mechanism, although that would lead one to expect higher calorimetry at that depth too. It is entirely possible that the distribution of *C. stylirostris* follows a pattern determined by a cline of some other as-yet-unknown variable. Perhaps *C. stylirostris* is generally a more localized species, while *C. alaskensis* is spread over a wider range of depths.

My third hypothesis - that the patterns in abundance and calorimetry of *Crangon* shrimp would be reflected in patterns of *A. medirostris* distribution - was not supported. The fact that sturgeon presence showed a null result with the two measurements of *Crangon* here examined does not necessarily mean that sturgeon distribution is not related to either of those variables: it is quite likely that the modeled presence of sturgeon was at too low of a spatial resolution compared with the relatively local scale of the *Crangon* data collected (Huff et al. 2012).

Potential flaws with this study include uneven sampling between different months, e.g. undersampling some months; as well as trying to relate modeled distribution probability of the large-scale sturgeon study to empirical data collected from a very localized area. In addition,

the need to eliminate data where samples for oxygen bombing were combined between different stations left relatively few remaining months for analysis of caloric density. A longer, more complete time series would have yielded a larger sample size from which to draw conclusions about seasonal caloric variation.

More enlightening results could have been uncovered if the number of gravid females in each tow sample had been recorded, as well as their dry mass and calorimetry. This would have been useful in confirming whether seasonal migration of *Crangon* is related to spawning.

Observing biomass density can give an overall picture of seasonal fluctuations in shrimp abundance, but the weakness of this measurement is that is assumes a uniform distribution of *Crangon* within the sampled area, and hence ignores patchiness of distribution, i.e. the tendency of marine animals in the water column to school in concentrated areas, a distribution often determined by food availability (Choat 1982). For example, our trawl area could have included the edge of a school at the beginning or end of the tow, but picked up little or no shrimp at other points in the same tow. Assuming an even spatial distribution and averaging the data out over the length of the tow might give an erroneous sense of there being a lower caloric density for that area.

More precise data could also have been gained if no samples had been preserved in ethanol prior to being weighed and desiccated. The mass adjustments for samples preserved in ethanol were carefully determined, but the data would have been even more precise if no adjustments had been needed at all. Finally, the survey protocol assumed that any bottom disturbance caused by the beam trawl would not affect subsequent results when returning to sample the benthos.

Conclusion

The hypothesis that depth and month each explain at least one measurement of *Crangon* abundance is supported. Based on these findings, it is likely that *Crangon* shrimp do experience some regular patterns in seasonal distribution, measured both in terms of their individual caloric density and in terms of their overall mass density. *C. alaskensis* was most common, and its abundance correlated positively with known nutrient fluctuations in the region. While no causal link for abundance can be established here, several factors could explain this pattern, including primary productivity, reproductive migration, and variations in size of an annual cohort. Limited data suggest that *C. stylirostris* reaches peak abundance later in the year than *C. alaskensis*, which could be due in part to resource partitioning between the species.

I was unable to find any relationship between *Crangon* abundance and sturgeon presence, meaning that the variations examined at this scale are unlikely to impact or be impacted by the general distribution of *A. medirostris*. There may still be some kind of significant ecological relationship between the sturgeon and its prey, but if such a relationship exists it could not be detected by this sampling protocol.

It is my hope that this investigation has shed a minor light on the habits of such understudied species. Future research is needed to elucidate the patterns hinted at by these findings. A better designed study would avoid such complications as ethanol preservation and cross contamination between calorimetry samples, and sample more regularly and consistently. In addition, in order to have a greater chance of detecting any relationships between the distribution of *Crangon* and *A. medirostris* - should they exist - sampling of *Crangon* would cover a wider area and at a spatial resolution more on the same scale as the sturgeon model.

I look forward to what future studies might uncover when the *Crangon* genus is given the coverage it currently lacks in the literature. As an important part of the near-shore trophic system of the north Pacific, it will be crucial to understand the phenological patterns of this and many other genera if accurate models are to be constructed to predict the impacts that a changing ocean will have on the intricate food webs it contains.

Acknowledgements

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