Marine Environmental Research 197 (2024) 106475

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Seasonal variability in energetic value of *Crangon alaskensis* and effects of marine heatwaves in the Northeast Pacific Ocean

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ARTICLE INFO

Keywords:
Crangon alaskensis
Northeast Pacific ocean
Marine heatwave
Caloric density
Energy
Biomass
Oregon

ABSTRACT

Research cruises were conducted to sample the invertebrate community along the shelf off the central coast of Oregon from 2010 to 2018. A large marine heatwave (MHW) hit the northeast Pacific in fall 2014 and persisted locally through 2015. Here, we assessed the caloric content changes of *Crangon alaskensis* (a common sandy shrimp) before, during, and after the 2014–2015 MHW. We found significant reductions in the caloric density of shelf populations of *C. alaskensis* during summer 2015. Oceanographic indices like the Biologically Effective Upwelling Transport Index (BEUTI) and the Pacific Decadal Oscillation (PDO) had greater predictive power for caloric density and biomass than *in situ* conditions, although bottom temperature and dissolved oxygen were also significantly correlated with caloric density. Caloric density of *C. alaskensis* was highest in 2018, indicating favorable conditions after the intense MHW of 2014–2015 allowed the caloric density to rebound.

1. Introduction

Brown shrimp, *Crangon* spp., are typically found in soft bottom cold temperate regions (Campos et al., 2012). *Crangon* spp. are important prey for many fish species (Henderson et al., 1992) including economically important flatfish (Campos et al., 2012). *Crangon crangon* are a relatively highly studied species in European waters because they are considered important prey (Tiews 1970), especially for flatfish (e.g. Henderson et al., 1992; Schückel et al., 2011, 2012) and whiting (Hamerlynck and Hostens 1993), as well as predators of both infauna (Bonsdorff and Pearson 1997) and epifauna (Sitts and Knight 1979; Gibson et al., 1995; Oh et al., 2001; Albaina et al., 2012) and are commercially harvested (Burukovsky & Ivanov 2015). Less research has focused on *Crangon* spp. in other regions since they are not commercially targeted. However, *Crangon* spp. play similar roles as both predators and prey worldwide; thus research is needed to understand their current and future ecological roles under changing ocean conditions.

Eleven members of the Crangonidae family are distributed on the Pacific coast of North America (Jensen 1995) with *Crangon alaskensis* (hereafter *C. alaskensis*) distributed throughout the range and having the broadest depth distribution: bays and estuaries to 275 m (Wicksten 1984, 2011). Importantly, in the NE Pacific, *Crangon* spp. are known prey for Green Sturgeon (*Acipenser medirostris*), an anadromous fish listed as vulnerable under the IUCN (IUCN 2014) and threatened under the US Endangered Species Act (Kelly et al., 2006; Israel and Klimley 2006). *Crangon* spp. are also one of the most important (by relative abundance) prey for Dungeness crab (Stevens et al., 1982), the highest value fishery in California, Oregon, and Washington (Pacific Fisheries Information Network [PacFIN], pacfin.psmfc.org). Most gut content analysis studies do not identify *Crangon* to species. As both benthic predators and prey for benthic and pelagic species, as well as their disturbance of bottom sediment during feeding and burrowing (Lloyd and Yonge 1947), *Crangon* spp. are important contributors to benthic-pelagic coupling (Griffiths et al., 2017).

The caloric content, or energy density, of prey organisms is important for the success of their predators. While variations in energy content of organisms relative to biomass can be driven largely by variation in lipids, caloric density takes potential variation of all elements of an organism into account, and, if coupled with estimates of biomass, can be used to estimate "potential energy" of organisms in an area (Gardner et al., 1985) and track how energy flows through a food web (Percy and Fife 1980). It has previously been shown that shrimp *(Sclerocrangon* spp.) have higher caloric densities than other marine invertebrates (i.e., polychaetes, cnidarians and echinoderms) making them a favorable prey item (Hondolero et al., 2012). While multiple papers report seasonal variability in the nutritional quality of benthic crustaceans (e.g., Morris

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https://doi.org/10.1016/j.marenvres.2024.106475
Received 22 December 2023; Received in revised form 14 March 2024; Accepted 23 March 2024

1971; Conover and Corner 1986; Gardner et al., 1985), Hondolero et al. (2012) reported no significant change in caloric densities of benthic invertebrates between the 1970's and 2000's. However, changes to temperatures (Liu et al., 2022) and PCO_2 (Wang et al., 2018) have been shown to have negative effects on decapod feeding efficiency, which is likely to affect their nutritional quality.

An unusual water mass developed in the NE Pacific Ocean during the winter of 2013–2014. Previously referred to as The Blob, the marine heatwave (MHW) (Hobday et al., 2016) was created by strong positive anomalies in sea level pressure, which led to a decline in cold-water upwelling (Gentemann et al., 2017). Upwelling is a seasonal process that allows cold, deep, nutrient rich water to come to the surface. The MHW built and sustained warmer waters that persisted at least through the summer of 2015 in the NE Pacific (Bond et al., 2015), with the positive PDO during this same period likely increasing the duration of the MHW in the region (Ren et al., 2023). In Oregon, sea surface temperature anomalies were not extended to the entire coastline until October 2014 and persisted through March 2015. Between March 2015 and May 2015, there was a reduction in magnitude of warm anomalies and return to normal sea surface temperatures along the coast (Gentemann et al., 2017). The MHW was sustained in other areas of the northeast Pacific through 2016, but there is evidence the large warm anomaly split into two parts in July 2015 which lead to colder sea surface temperatures off Washington and Oregon and warmer sea surface temperatures off California (Fewings and Brown 2019). From July 2015 to April 2016, there were uniform warm anomalies, but they were not as extreme as the previous years. After the upwelling of May–July 2016, the warm anomalies were entirely absent north of Cape Mendocino (Gentemann et al., 2017). A review on the California Current System suggested above average sea surface temperatures appeared again and persisted through early 2017 confirmed by a southern copepod assemblage instead of a northern one (Wells et al., 2017). In 2018, sea surface temperatures north of Point Conception were considered normal and the Pacific Decadal Oscillation (PDO) was positive for the majority of the year (Thompson et al., 2019).

While *Crangon* spp. are thought to be tolerant to warmer temperatures (Campos et al., 2012), reduction of upwelled waters can have other detrimental effects. Variation in upwelling can affect the timing and magnitude of phytoplankton blooms due to low nutrient availability restricting growth rates of phytoplankton (Pedersen and Borum 1996), which can have cascading effects throughout the food web, potentially affecting *Crangon* spp. due to variability in the abundance or quality of their food sources. Recent studies in the NE Pacific Ocean found reduced body length and reduced growth of krill (*Euphausia pacifica* and *Thysanoessa spinifera;* Killeen et al., 2022; Dorman et al., 2023) and reduction in nutritional value of Pacific sand lance (von Biela et al., 2019) linked to the 2014–2016 MHW.

MHWs are predicted to increase in frequency and duration across the 21st century (Oliver et al., 2019) coupled with global warming (Frolicher et al., 2018). The overall objective of this study was to assess seasonal variability in caloric content of *Crangon alaskensis* and to determine if MHW years impacted expected seasonal patterns. We hypothesized the caloric densities of the shrimp would be lowest during the peak of the MHW in 2015 in Oregon compared to the other years due to the combination of temperature and nutritional stress.

2. Materials and methods

2.1. Collection techniques/sample processing

Shelf populations of *Crangon* spp. were sampled three to five times per year from June 2010 to August 2015 as part of a project to characterize benthic communities near Newport, Oregon (OSU, 2019). That project ended in 2015, and there was no collection of invertebrates in 2016. From May 2017 to November 2018, samples were collected 6 times per year by National Oceanographic and Atmospheric Administration (NOAA) Fisheries' National Cooperative Research Program and Northwest Fisheries Science Center with administrative support provided by the Pacific States Marine Fisheries Commission. For the purposes of this study, we are describing before heatwave years as 2010–2014, the during heatwave year as 2015 and after heatwave years as 2017–2018 due to the timing of our collections (Supplemental Table 1) in relation to when the warm water anomalies persisted off central Oregon as described in the studies above.

Specimens were collected by a beam trawl (2-m wide, with a 3-mm liner for the net in the cod end). Each beam trawl tow lasted five or 10 min. From 2010 to 2015, three separate lines (BB, MB, NH) were sampled, each at 30-, 40- and 50-m depths for a maximum of 9 samples per trip in the initial time series (not all stations were successfully sampled on each date); in 2017 and 2018, two different stations on the NH line (NH3 & NH5, at 50 and 60 m depths respectively) as well as BB40 and MB40 were sampled (Fig. 1), but not all four stations were sampled each time due to limited personnel or local weather constraints. These 11 stations spanned 7.5 km cross-shelf distance and 8.5 km alongshore and are considered replicates within the site as initial analyses (Danilchik et al. 2015) indicated no significant differences in biomass or caloric density across the sampled depths. At each station, a CTD was cast to collect temperature, salinity, oxygen, fluorescence, and other environmental data. A total of 227 trawl collections were made from 2010 to 2018.

In 2010–2015 all the invertebrates collected in each trawl were bagged and flash frozen in a cooler with dry ice on board the vessel immediately after collection. In 2017 and 2018, large collections of invertebrates were sub-sampled (with varying precision) on board and then bagged and placed on dry ice. Frozen samples were later thawed and sorted by species in the lab. *C. alaskensis* were found in nearly every

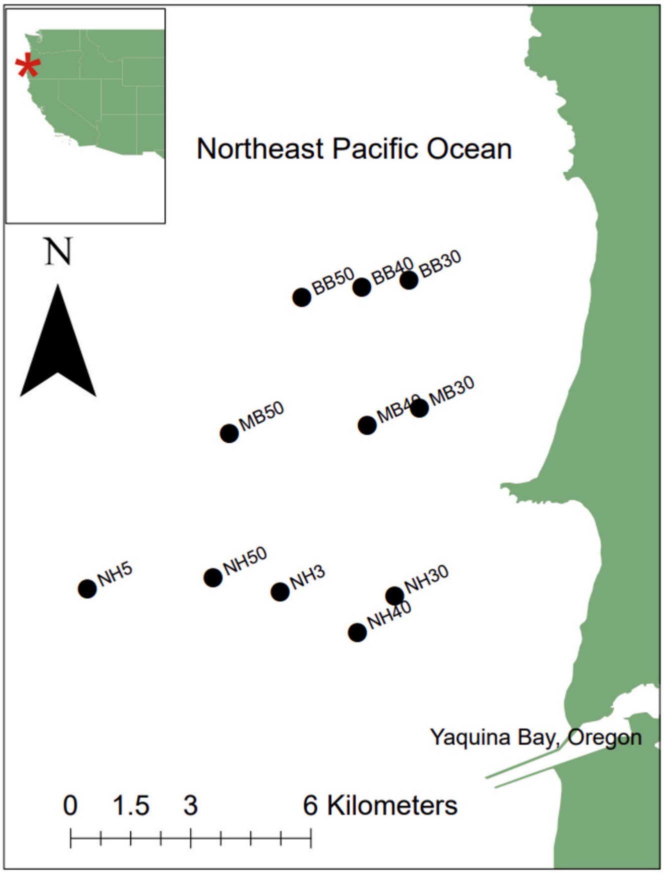

Fig. 1. Study area with station locations for trawl surveys on the central Oregon coast, USA.

collection in varying densities; other *Crangon* species were too infrequently collected to enable analysis.

2.2. Biomass

Each station for each sampling date represents one sample for biomass. After thawing and sorting, some samples were stored in 70% ethanol while others were immediately dried in a drying oven for 48–60 h at 60 °C, weighed for biomass calculations, and saved for bomb calorimetry. Those that were stored in EtOH were later dried and weighed. We determined an average of 33% dry mass may be lost due to preservation (Danilchik et al. 2015) and adjusted the biomass values for those samples accordingly. Total biomass for each trawl collection was scaled up to account for subsampling if necessary and then divided by the area trawled (as determined by a meter wheel on the beam trawl frame). Biomass was not calculated for 2018 due to missing trawl wheel turns and imprecise subsampling procedures onboard; thus 208 biomass samples are reported for 2010 to 2017.

2.3. Parr bomb calorimetry

Bomb calorimetry is one of the most used methods to determine the energy content of an organic organism. Each station for each sampling date (with sufficient numbers of *Crangon alaskensis* for bomb calorimetry) represents a single sample. Each sample was run in duplicate or triplicate for bomb calorimetry and the average was used as a single point for that station and sampling date. A total of 184 samples,(See Supplemental Table 1 for distribution across months and years), were analyzed for caloric density in an oxygen bomb calorimeter (Parr Model 1341). After drying for biomass calculations, samples were ground to a homogeneous powder with a mortar and pestle. Each individual bomb sample was weighed to approximately 1 g and placed into a combustion chamber filled with oxygen to 30 atm. The entire combustion chamber was placed in 2000 g of deionized water. The sample was ignited and the subsequent temperature rate of change (along with measuring the remaining weight of any uncombusted material) was used to calculate caloric density (joules g^{-1} dry weight).

2.4. Data analysis

Data were analyzed to determine if they met parametric test assumptions (e.g., normal distribution). A two-way crossed ANOVA was used to test if the caloric density of *C. alaskensis* varied significantly by year and month 2010–2018 (no 2016 data). A Tukey HSD was used to examine pairwise comparisons. A one-way Kruskal-Wallis was used to test if the biomass of *C. alaskensis* varied significantly by year and month separately for 2010–2017 (no 2016 or 2018 data). A post-hoc Dunn test was used to examine pairwise comparisons for non-parametric data.

Caloric density anomalies were calculated for months that had a minimum of five years of data (June, August, and October) to check for statistical differences. A total mean for each of the months (June, August, and October) across all years were calculated and then each year was individually analyzed to see how it deviated from the total mean. A Shapiro-Test was used to test for normality of calculated anomaly data. For each month, a one-way ANOVA was used to test if anomalies of caloric density of *C. alaskensis* shrimp significantly varied by year from 2010 to 2018. A Tukey HSD test was used to examine pairwise comparisons of the anomaly data between years.

Monthly climate and upwelling indices: NOAA PDO (https://www.ncei.noaa.gov/access/monitoring/pdo/), the Biologically Effective Upwelling Transport Index (BEUTI) (https://mjacox.com/upwelling-indices/), the Coastal Upwelling Transport Index (CUTI), the Multivariate ENSO Index Version 2 (MEI.v2) (https://psl.noaa.gov/enso/mei/) and the Traditional Bakun Calculated Upwelling Index (https://oceanwatch.pfeg.noaa.gov/products/PFELData/upwell/monthly/upindex.mon) were downloaded for each month of sampling for comparison to caloric density and biomass. To account for a delay in response, we also tested relationships to climate indices one month and two months before the sampling took place. Multiple linear regression was used to test which *in situ* (from the CTD) environmental variables and/or regional indices best predicted caloric density and biomass of shelf populations of *C. alaskensis*. Models were run for *in situ* parameters only and then with *in situ* plus each of the climate/upwelling indices. Liner mixed models including station as a factor were tested, but station was never significant and model performance was worse. All models were significant, so final model selection was based on the combination of *in situ* and downloaded parameters that resulted in the highest R^2 and lowest AIC. Environmental variables that were significant in the full model were then individually regressed against the *C. alaskensis* caloric density or biomass to investigate the strength and sign of the relationship. We compared biological spring transition data from NOAA Fisheries (https://www.fisheries.noaa.gov/west-coast/science-data/local-biological-indicators#biological-spring-and-fall-transitions) and compared it to our sampling dates. All statistical tests were run in RStudio (Version: 2023.3.0.386, Posit team, 2023).

3. Results

3.1. Caloric density

Caloric density of shelf populations of *C. alaskensis* averaged 17,704 J g^{-1} dry weight and varied significantly by month, year, and the interaction of month and year (Two-Way Crossed ANOVA: p-values <0.005; Table 1), ranging from 12,991 to 21,818 J g^{-1} dry weight. 2018 was significantly different from 2012, 2014 and 2015 (TukeyHSD: p-values <0.001). All other year pairwise comparisons were not significantly different (p-values >0.05). Typically, there was an increase in caloric density from June to August followed by a decline in October (Fig. 2). Our limited winter data indicate caloric densities stayed low and then increased in the spring months with variability of the timing of that increase among years. Among months, December was significantly lower than all other months (TukeyHSD: p-values <0.05) except October (p-value = 0.362) (See Supplemental Table 2 for full Tukey table). Further, October was significantly different from June, August, and September (TukeyHSD: p-values <0.05). All other month pairwise comparisons were not significantly different (p-values >0.05).

The general seasonal pattern differed in 2015 and 2017 where caloric densities decreased from June to August (Fig. 2; Fig. 3). Tukey HSD results indicated there were no significant differences between all pairwise comparisons of mean August caloric density of *C. alaskensis* shrimp across all the years (Tukey HSD for interaction of month and year: all August-to-August comparisons between 2010 and 2018 p-values >0.30). When we calculated August anomalies in caloric density (as compared to the dataset mean), three years (2014, 2015, and 2017) had a median anomaly value below zero while four years (2010, 2011, 2013, and 2018) had a median anomaly value above zero (Fig. 4). A one-way ANOVA revealed statistically significant differences in August anomalies for caloric density among years (df = 6, f-value = 13.79, p < 0.001): 2014 was significantly lower than 2013 and 2018 (p < 0.001), and 2015 was significantly lower than 2010, 2011, 2013 and 2018 (p < 0.05; Table 2). The mean values of August anomalies in 2018 were significantly higher than the other positive years (2011 and 2017: p-

Table 1
Results of two-way crossed analysis of variance to test for significance of year and month on caloric density of *C. alaskensis*.

	Df	Sum sq	Mean sq	F value	Pr (>f)
Month	7	95729130	13675590	9.692	<0.001*
Year	7	64016139	9145163	6.482	<0.001*
Month × year	20	77098374	3854919	2.732	<0.001*
Residuals	149	2.1 E+08	1410957		

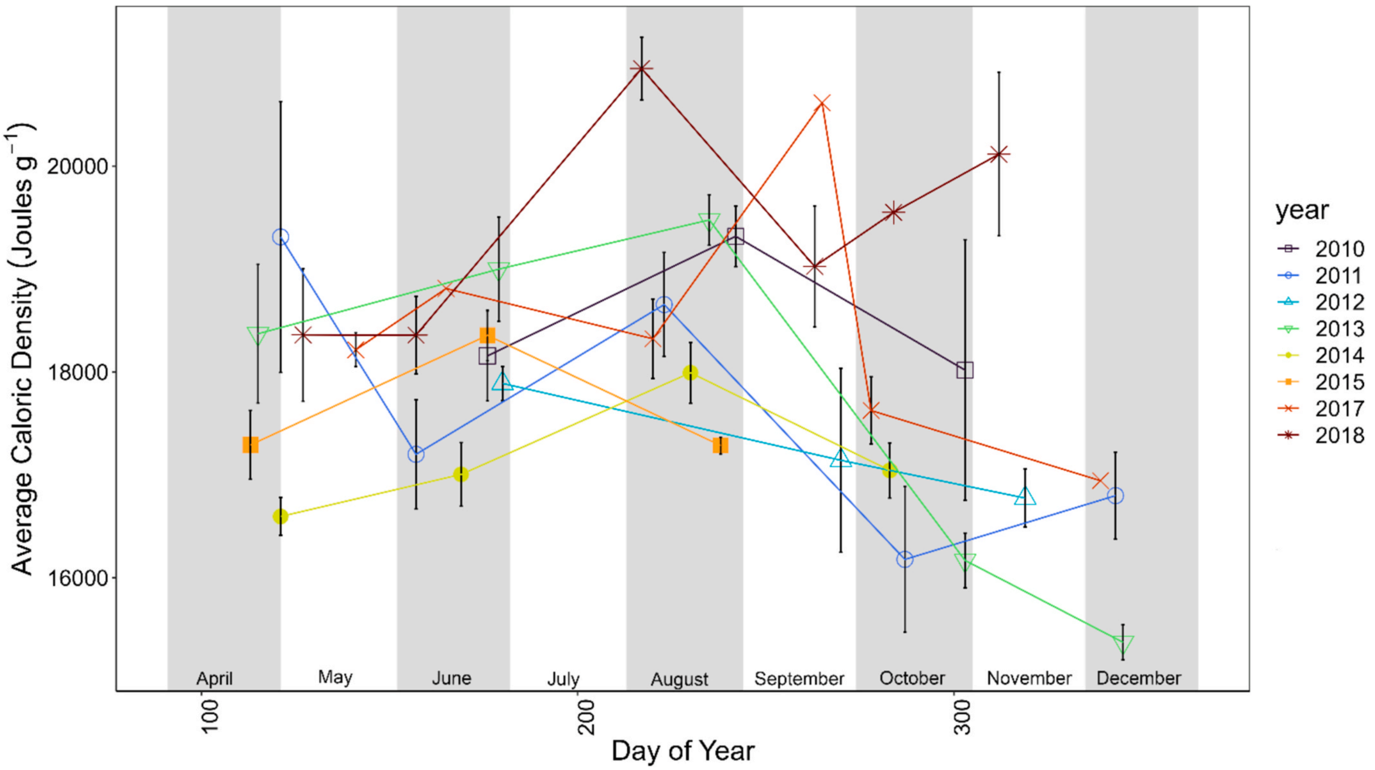

Fig. 2. Caloric density (joules g^{-1}) by day of year of shelf populations of *C. alaskensis*. Error bars are ± standard error. Symbols indicate year.

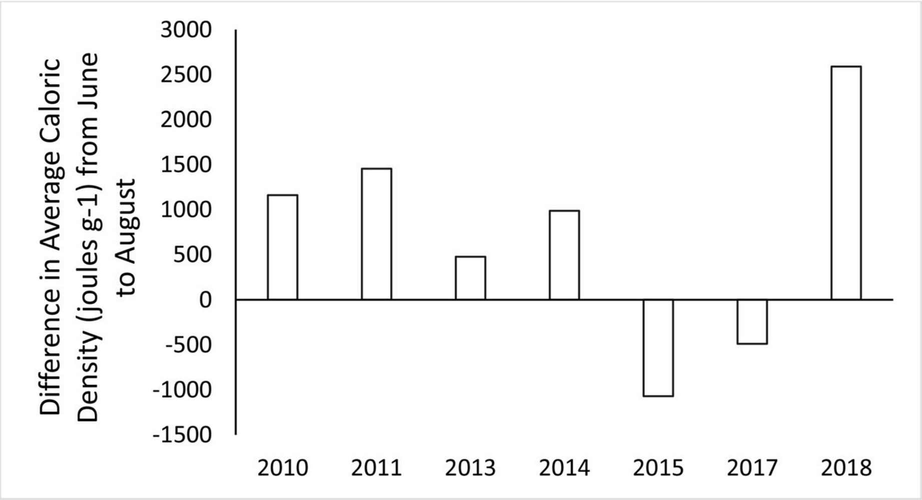

Fig. 3. Difference in average caloric density (joules g^{-1}) of shelf populations of *C. alaskensis* from June to August for each year.

values <0.05; Table 2). All other years of mean August anomaly caloric density values were not significantly different (p-values >0.05; not shown).

We also calculated June and October anomalies in caloric density (as compared to the dataset means for each month). June 2011 and 2014 had negative anomaly values while five years (2010, 2013, 2015, 2017 and 2018) had positive anomaly values (Supplemental Fig. 1). A one-way ANOVA revealed statistically significant differences in June anomalies for caloric density among years (df = 7, f-value = 3.774, p = 0.003). Among years, 2013 (p-value = 0.001) and 2015 (p = 0.04) were both significantly higher than 2014 but all other years of mean June anomaly caloric density values were not significantly different (p-values >0.05). October anomalies in caloric density were all close to zero (Supplemental Fig. 1) and did not differ significantly among years (one-way ANOVA, df = 5, f-value = 02.352, p = 0.076).

Multiple linear regression analysis indicated the model that included the *in situ* data, depth, BEUTI with a one month delay as the upwelling index and PDO as the climate index had the strongest predicting power of caloric density over all other combinations with the different upwelling indices and climate indices (multiple $R^2 = 0.279$). The *in situ* bottom temperature, bottom dissolved oxygen, and the BEUTI with a one-month delay each were significant terms in the model in predicting caloric density of *C. alaskensis* (p-values <0.05; Table 3) with the one-month delay of the BEUTI having the lowest p- and highest t-values. While depth, bottom salinity, and fluorescence themselves were not significant within the model, the R^2 was reduced and AIC increased by

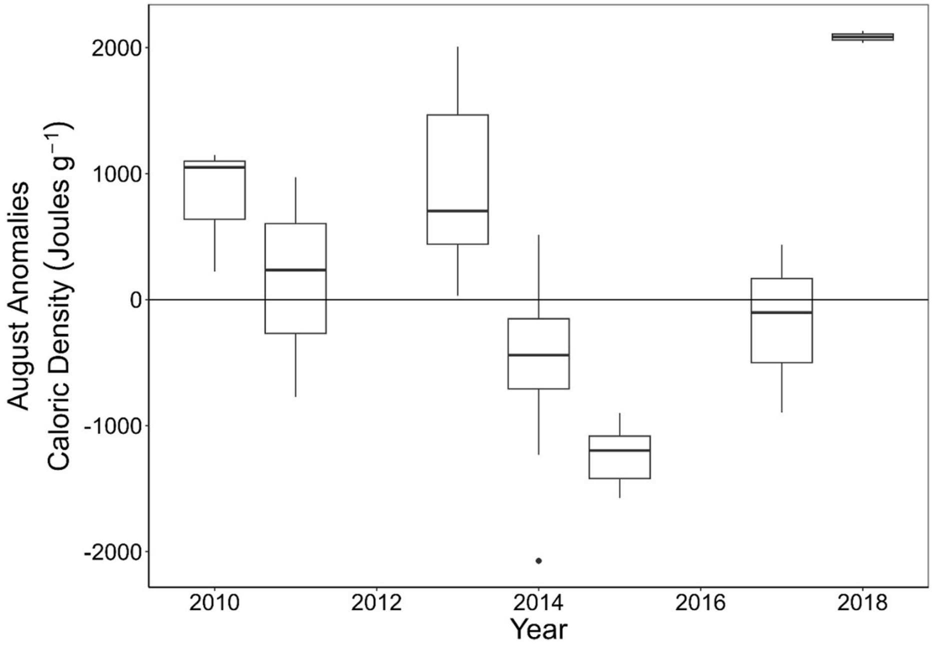

Fig. 4. August anomalies of caloric density (joules g^{-1}) of shelf populations of *C. alaskensis* by year. No August data for 2012 and 2016.

Table 2
Tukey HSD results for all significant pairwise comparisons of years for August anomalies only.

	DIFF	LWR	UPR	P ADJ
2014–2013	−1484.56	−2480.37	−488.76	<0.001
2015–2010	−2031.84	−3398.07	−665.605	<0.001
2015–2011	−1369.05	−2735.28	−2.81804	0.049
2015–2013	−2191.2	−3157.27	−1225.13	<0.001
2018–2011	1939.51	68.72163	3810.297	0.038
2018–2014	2601.917	981.767	4222.067	<0.001
2018–2015	3308.558	1706.511	4910.605	<0.001
2018–2017	2271.914	401.1265	4142.702	<0.01

Table 3
Multiple linear regression results to test which of the environmental variables and indices best predicted caloric density of *C. alaskensis* shrimp.

	Estimate	Std. error	T value	Pr (>$\lvert T \rvert$)
Intercept	−3502.64	11989.94	−0.292	0.771
Bottom Temperature	615.791	195.171	3.155	0.002*
Bottom Salinity	504.197	329.015	1.532	0.127
Bottom Fluorescence	−15.826	18.609	−0.85	0.396
Bottom Dissolved Oxygen	−534.12	133.47	−4.002	<0.001*
Depth	7.256	12.839	0.565	0.573
BEUTI (one month delay)	304.744	59.468	5.125	<0.001*
PDO	157.051	90.574	1.734	0.085

removing them, so they are included in the final model. Among the three significant environmental predictors, the correlation between the BEUTI with a one-month delay and caloric density of *C. alaskensis* was the strongest (SLM: p-value <0.001) and slightly positive ($y = 1.74 \times 10^4 + 294x$, $R^2 = 0.15$; Fig. 5); individual correlations with temperature, dissolved oxygen and the PDO were much weaker and slightly negative (Supplemental Figs. 2–4). Bottom salinity and bottom fluorescence were not significant predictors of caloric density (MLR: p-values >0.10; Table 3).

3.2. Biomass

Biomass data did not pass normality assumptions and were log-transformed. Log-transformed biomass of shelf populations of *C. alaskensis* varied significantly by year (Kruskal-Wallis Test: chi-squared = 20.319, df = 6, p-value = 0.002) with 2015 significantly higher than all other years (Table 4), this is potentially due to the lack of winter biomass data for 2015. All other year pairwise comparisons were not significantly different (p-values >0.05). Log-transformed biomass of shelf populations of *C. alaskensis* varied significantly by month (Kruskal-Wallis Test: chi-squared = 55.044, df = 7, p-value <0.001). Across all years, there was a general trend of biomass increasing from the spring to the summer months and declining from the fall into the winter (Fig. 6). There was a notable steep decline in 2013 from April to June, but it increased in August (Fig. 6). December and November were significantly different from five months including April, May, June, August, and September (p-values <0.01). October was significantly different from April, June, and August (p-values <0.01). All other month pairwise comparisons were not significantly different (p-values >0.05, see Supplemental Table 3).

Multiple linear regression analysis indicated the model that included the *in situ* data, BEUTI with a one month delay as the upwelling index and PDO as the climate index had the strongest predicting power for log-transformed biomass over all other combinations with the different upwelling indices and climate indices. Bottom temperature, BEUTI with a one-month delay, and the PDO each were significant predictors in the model for biomass of *C. alaskensis* (p-values <0.03; Table 5) with the PDO having the lowest p- and highest t-values. The relationship between the BEUTI with a one-month delay and log-transformed biomass of *C. alaskensis* was significant (SLM: p-value = 0.00006) but the correlation was weak ($y = -4.45 + 0.177x$, $R^2 = 0.08$; Fig. 7). The influence of PDO (SLM: p-value = 0.325) on biomass was weak but when modeled with other variables the correlation strength and significance increased. There was a significant (SLM: p = 0.00004) slightly positive relationship between biomass and caloric density (Fig. 8).

4. Discussion

Crangon spp. are sandy bottom shrimp that spend the majority of their life on the benthos where they can be categorized as benthivores due to the sand grains found in their guts (Schmidt et al., 2021), targeting both infaunal and epifaunal (Sitts and Knight 1979; Wahle 1985; Bonsdorff and Pearson 1997; Jarrin and Shanks 2008; Maher et al.,

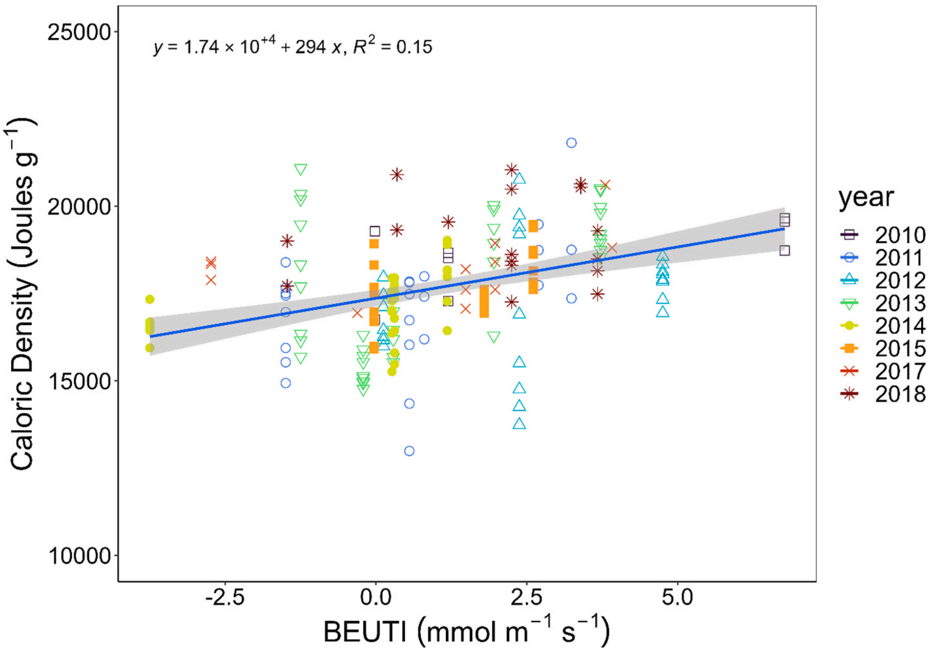

Fig. 5. Caloric density (joules g^{-1}) versus the BEUTI (mmol m^{-1} s^{-1}) from the month before the sampling date.

Table 4

Dunn test results for significant pairwise comparisons of years for log-transformed biomass.

	Z	P. Unadj	P. ADJ
2010–2015	−2.86369	4.19E-03	0.022
2011–2015	−2.52341	1.16E-02	0.041
2012–2015	−3.46305	5.34E-04	0.006
2013–2015	−3.99181	6.56E-05	0.001
2014–2015	−2.80734	5.00E-03	0.021
2015–2017	2.914716	3.56E-03	0.025

2013) prey, including newly settled flatfish (e.g. Gibson et al., 1995; Oh et al., 2001; Taylor 2003; Albaina et al., 2012). In the northeast Pacific *Crangon* spp. are prey for economically important species such as Green Sturgeon (Kelly et al., 2006; Dumbauld et al., 2008) and Dungeness crabs (Stevens et al., 1982) and likely are important prey for flatfish (e.g. Henderson et al., 1992; Schückel et al., 2011, 2012) and potentially whiting (Hamerlynck and Hostens 1993) as has been found for *Crangon crangon*. Thus, we sought to quantify and determine if there were seasonal trends in the abundance (reported as biomass) and caloric density (food values) of the most common *Crangon* on the mid-shelf, *Crangon alaskensis,* and to assess whether variations in biomass and caloric density were linked. From 2010 to 2018 we detected similar trends in *C. alaskensis* caloric density and biomass on the mid-shelf, both of which increased from spring into summer and declined from the summer into the fall and winter. Overall, our determinations of caloric content of NE Pacific *Crangon alaskensis* (17,704 J g^{-1} dry weight) are substantially higher than that reported for the commercially important *C. crangon* in the North Sea (14,000 to 17,000 J g^{-1} dry weight; Hufnagl et al., 2010).

Our findings of seasonal patterns in caloric density are in contrast to the seasonal patterns for *C. crangon* in the Wadden Sea (North Sea) which had the lowest caloric content in September, increasing over winter to a maximum in spring, potentially due to vitellogenesis (Hufnagl et al., 2010). The summer peak in caloric density observed in this study does not appear to be related to high occurrence of egg-bearing females in summer, as related species from the Oregon central coast (*C. nigricauda* and *C. franciscorum*) both have spawning periods of December–March and April–August (Krygier 1973), if *C. alaskensis* have a similar reproduction cycle which is unknown (Campos et al., 2012). However, the summer peak of caloric density of NE Pacific *C. alaskensis* is similar to that observed for the anomuran crab, *Munida subrugosa,* in the subantarctic, which had the highest energetic content in the summer after the period of seasonal reproduction and feeding (Romero et al., 2006). We also anticipate the summer peak is driven by food availability driven by the transition to upwelling conditions in the spring.

Seasonal variability in biomass could be due to changes in body size of individuals or changes in numbers of individuals due to recruitment or migration and our overall pattern was similar to *C. crangon* observations off southern England where abundances were low in winter and reached high levels in late summer and early fall (Moore et al., 1979). If *C. alaskensis* follow similar migration patterns to *Lissocrangon stylirostris* in Oregon where mature adults migrate out onto the continental shelf to spawn in summer and fall and move back to the shorelines and estuaries (which we did not sample) in the spring (Jarrin and Shanks 2008), our observed differences could be related to changes in horizontal distribution. A limitation of this study is we only sampled from the bottom at depths between 30 and 60 m and it is possible *C. alaskensis* migrated vertically out of these depths during the study in response to temperature as has been observed for *C. crangon* (Jeffery and Revill, 2002), Little is known about recruitment timing for *C. alaskensis* therefore we are unable to determine if our variations in biomass are driven by recruitment.

According to our analysis of environmental factors, both measures of *C. alaskensis* productivity seem to be driven (at least in part) by upwelling as BEUTI with a one-month lag (which is strongly coupled with temperature) was the strongest abiotic predictor of *C. alaskensis* caloric density while for biomass it was the second strongest abiotic predictor following the PDO. The higher biomass and caloric density in late summer are likely a result of summer upwelling of cold, nutrient rich water triggering primary productivity in the form of photosynthesis, and thus greatly increasing available energy in the system through the summer in the form of greater food abundance (Small and Menzies 1981; Varela and Harrison 1999; Whitney et al., 2005). This likely bottom-up control of *C. alaskensis* populations in the NE Pacific supports that hypothesized for *C. crangon* in the English Channel (Amara and Paul 2003) and Wadden Sea (Kuipers and Dapper 1981; Hufnagl et al., 2010). The PDO was the highest predictor for biomass, mirroring the findings of Campos et al. (2010) who found that the North Atlantic Oscillation

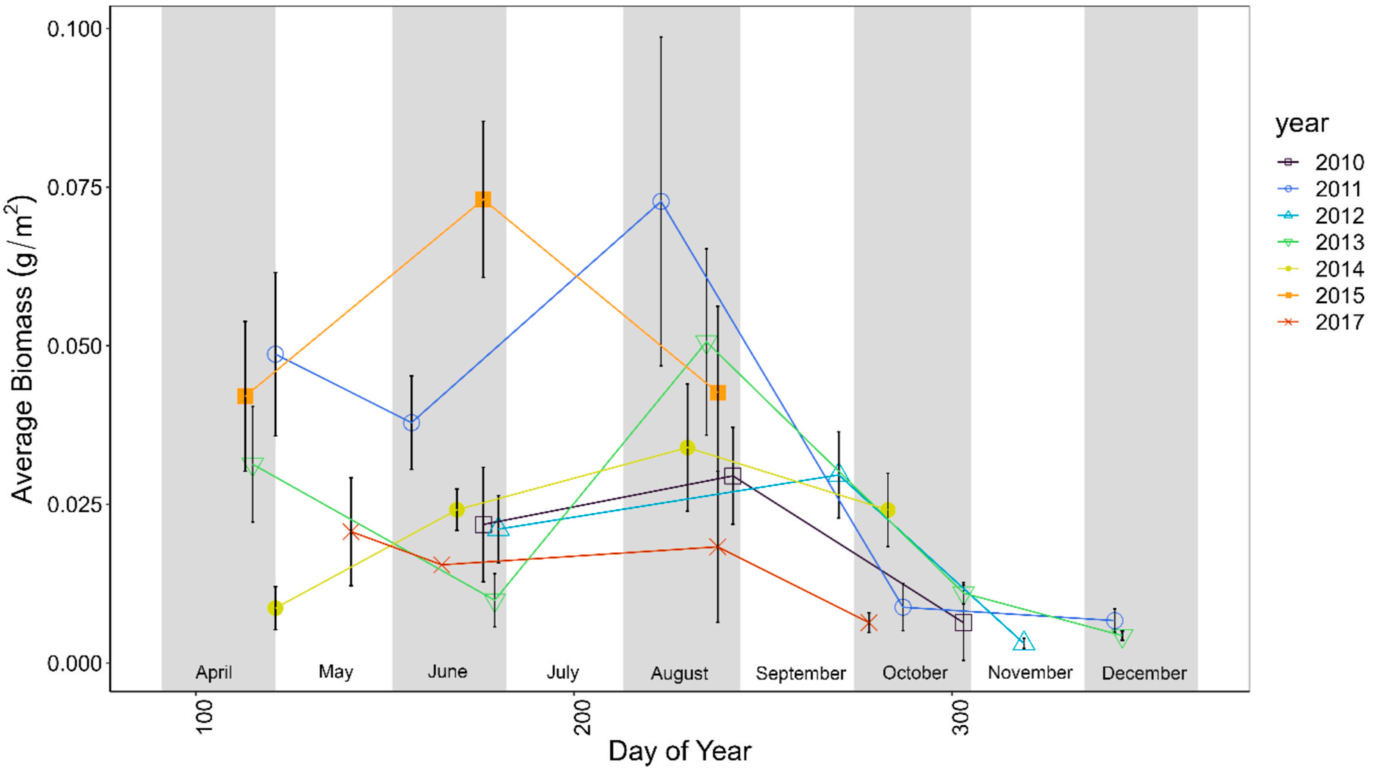

Fig. 6. Average biomass (dry g/m^2) by day of year of shelf populations of *C. alaskensis* from 2010 to 2017. Accurate biomass data were not available for 2018 as collections were subsampled on board. Error bars are ± standard error. Symbols indicate year.

Table 5
Multiple linear regression results to test which of the environmental variables and indices best predicted log-transformed biomass of shelf populations of *C. alaskensis* shrimp.

	Estimate	Std. Error	T-value	Pr (>|T|)
Intercept	−4.59729	9.92367	−0.463	0.644
Bottom Temperature	−0.46795	0.1789	−2.616	0.010*
Bottom Salinity	0.13882	0.26866	0.517	0.606
Bottom Fluorescence	0.00334	0.01571	0.213	0.832
Bottom Dissolved Oxygen	−0.07645	0.11883	−0.643	0.521
BEUTI (one month delay)	0.10079	0.04543	2.218	0.028*
PDO	0.233	0.07125	3.27	0.001*

Index (NAOI) was significantly correlated with both spring and fall abundances across years (each season tested separately) in European populations.

Temperature was also significant in both the caloric density and biomass models potentially due to its direct effects on energy loss in *Crangon* (*C. septemspinosa*; Taylor and Peck 2004) beyond the bottom-up trophic effects triggered by variability in upwelling. Stressful oxygen levels have been demonstrated to reduce predation rate in *C. crangon* (Sandberg et al., 1996), which could be the mechanism behind the significant effect of dissolved oxygen on caloric density in the model. While included in the best models, salinity was not a significant factor in the models for either caloric density or biomass likely because *C. alaskensis* is euryhaline, being distributed in both estuaries and on the shelf (Wicksten 1984, 2011). We did not see a significant effect of bottom fluorescence on caloric density or biomass because of the limited range of values; surface fluorescence may be a more relevant factor to consider due to the likely role of phytoplankton in linking upwelling variability to upper trophic levels.

Analyses here suggest the MHW that hit the Pacific Northeast in late 2014 with a peak in 2015 had negative impacts on the expected summer peaks in caloric density and biomass of *C. alaskensis*, similar to impacts reported for krill (Killeen et al., 2022; Dorman et al., 2023) and Pacific sand lance (von Biela et al., 2019). 2015 and 2017 were the only years that had declines in caloric density from June to August. Further, the August anomalies displayed 2014, 2015 and 2017 all falling below the total average of caloric density. Additionally, the variability was lowest in 2015, particularly in August, indicating a much more uniform condition for the population as compared to none MHW years. We hypothesize that the mechanism by which the MHW affected the expected summer peak in caloric density of *C. alaskensis* may have been via impacts on the biological spring transition. The physical spring transition for the northeast Pacific is when the winds begin to blow primarily from the north and the coastal currents flow south. The spring transition usually coincides with a change from downwelling to upwelling. There is a delay between when the currents and the zooplankton composition change, so researchers use a 'biological spring transition' for tracking ecological impacts. Between 2010 and 2014, the average day the biological spring transition began was around day 111 which is mid-April while in 2015 and 2016, NOAA reported no biological spring transition indicating the zooplankton community did not change to the colder northern species. Thus, the prey source for *C. alaskensis* was not replenished as previous years and there was less to sustain previous numbers so their caloric density and biomass was negatively impacted. In addition to the MHW resulting in a stratified water column that dampened upwelling, delaying the biological spring transition, the nutrient stress also apparently triggered a toxic phytoplankton bloom by the diatom Pseudo-nitzschia (Du et al., 2016) which may have had further bottom-up effects we were not able to capture.

In 2017 the biological "spring" transition was determined to be July 12, which is much later than expected and may explain why we also saw negative August anomalies that year as well, even though a MHW was not recorded. The cold-water copepods were only present for 84 days (almost half the normal duration in years prior to the MHW) *C. alaskensis* likely begin to store energy for reproductive purposes before this date and the delayed start in the biological spring transition likely had a

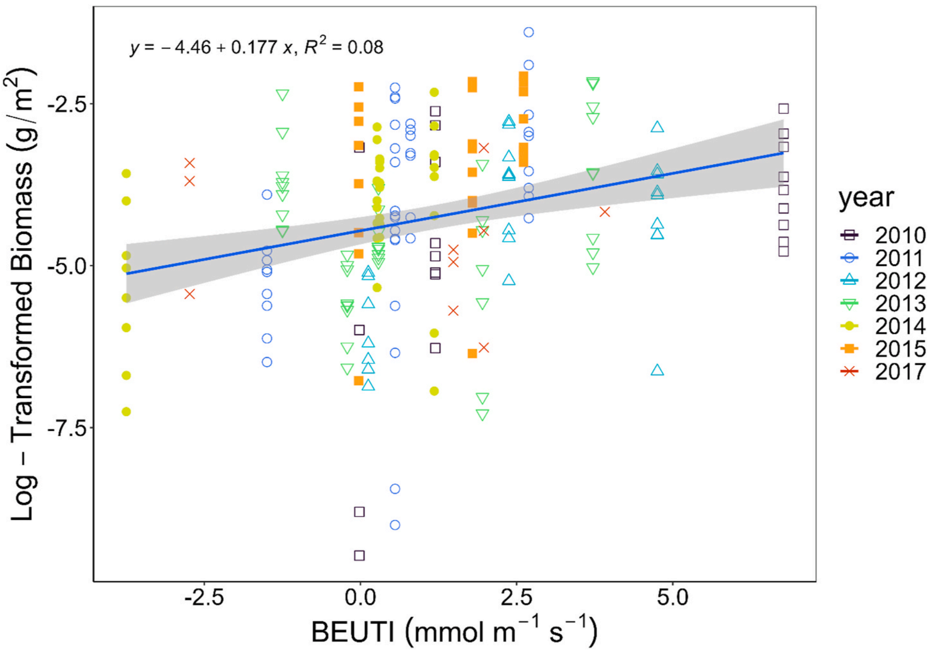

Fig. 7. Log-transformed biomass (dry g/m^2) versus the BEUTI (mmol m^{-1} s^{-1}) from the month before the sampling date.

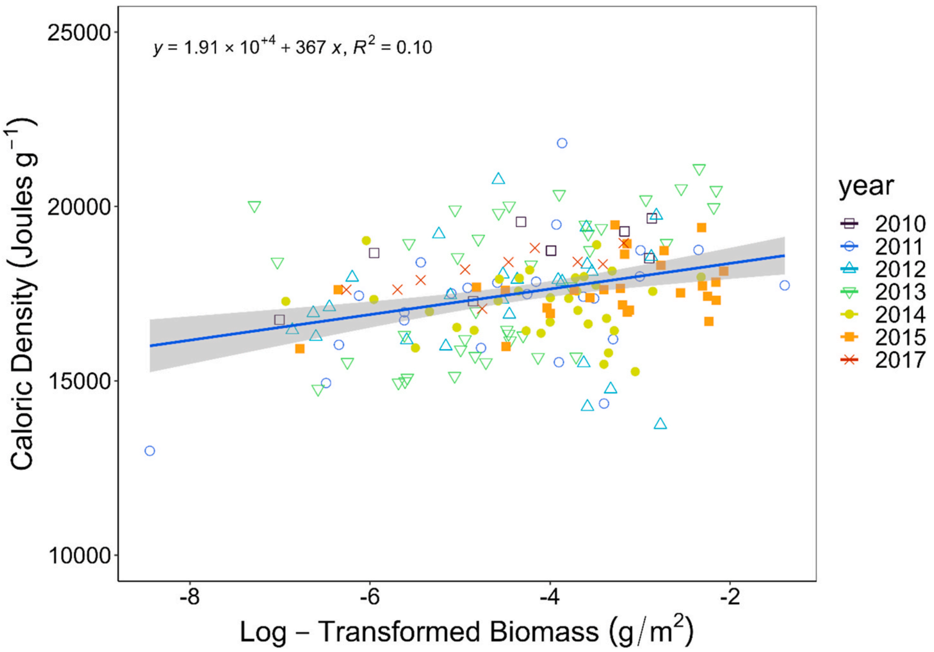

Fig. 8. Caloric density (joules g^{-1}) versus log-transformed biomass (dry g/m^2).

negative impact on their caloric densities. In 2018, the biological spring transition day was May 29. This return to the transition being in the spring might be why we saw the caloric density rebound in that year. Other research has reported large increases (>30%) in krill biomass in 2018 compared to previous years (Dorman et al., 2023) indicating 2018 was a very productive year for the entire system. We saw the highest caloric densities during 2018 especially in the August anomaly results. The right conditions allow for the caloric densities to rebound and the entire food web likely benefits.

Gut content analyses on Dungeness crabs indicated *Crangon* spp. were most predated upon at night and during the winter and spring (Stevens et al., 1982) which is the same seasons we saw *C. alaskensis* to be the least abundant and the least calorically dense. Two potential reasons for this observed pattern are that Dungeness crabs are not targeting *Crangon* spp. when they are most abundant/calorically dense or they are inflicting a substantial amount of predation pressure on *Crangon* spp. during this time as seen with other predators on *Crangon crangon* (Campos et al., 2010), suggesting a top-down influence on population size. In a separate more recent study, researchers found more decapods in the guts of Dungeness crabs during the summer compared to other months (Harbison et al., 2022) but did not distinguish between *Crangon* and other decapod species. Our results here indicate reduced caloric densities of *C. alaskensis* during MHWs may directly impact their predators through reduced energy consumption. During periods of lower caloric density in *C. alaskensis*, predators like Dungeness crabs likely will have to spend more energy eating and searching for food instead of reproducing which can have repercussions on future population size.

4.1. Conclusions

Crangon spp. are very abundant in the northeast Pacific and in Alaskan estuaries *C. alaskensis* has been one of the most abundant invertebrates captured (Miller et al., 2014); however little research has investigated patterns of abundance or condition of this important predator and prey species. Furthermore, field studies on the effects of MHWs on crustaceans is lagging behind other taxonomic groups (Joyce et al., 2024), despite decapod crustaceans' increasing importance in global fisheries (Boenish et al., 2022). The results here indicate MHWs and associated absence, or delay of the biological spring transition negatively impact the biomass and caloric density of *C. alaskensis*. The same oceanographic process that prohibited the cold-water zooplankton assemblage from forming in 2015 (and severely delayed it in 2017) also likely impacted the ability of *C. alaskensis* to accumulate lipids (that have a higher energy unit per dry weight), which may have consequences for their reproductive capacity (a notable gap in MHW research; Joyce et al., 2024) and the success of their predators. However, our findings indicate biomass and caloric density of *C. alaskensis* can rebound following a large MHW event.

CRediT authorship contribution statement

Angelina N. Zuelow: Writing – review & editing, Writing – original draft, Project administration, Methodology. **Nikolai M. Danilchik:** Project administration, Methodology. **Hope S. Donahue:** Project administration, Methodology, Formal analysis. **Sarah K. Henkel:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Funding from OWET and USDOE. NOAA NWFSC including W.W., A. J.P., J.F., Captains and crew of R/V Elakha, and many undergraduates who helped sort samples. REU support (Zuelow 2017; Donahue 2022) from NSF OCE REU Awards 1263349 and 1758000, respectively.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106475.

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