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Dietary and spatial overlap among jellyfish and small pelagic fish in the eastern Bering Sea during recent marine heatwave conditions

M. B. Decker^{1,*}, R. D. Brodeur², E. Fergusson³, W. Strasburger³, K. Cieciel⁴¹Department of Ecology & Evolutionary Biology, Yale University, New Haven, CT 06520, USA²Hatfield Marine Science Center, Oregon State University, Newport, OR 97365, USA³Auke Bay Laboratory, NOAA Alaska Fisheries Science Center, Auke Bay, AK 99801, USA⁴NOAA National Marine Fisheries Service, Alaska Regional Office, Juneau, AK 99802, USA

ABSTRACT: Populations of scyphozoan jellyfish in the eastern Bering Sea (EBS) can grow rapidly within a single season and have fluctuated widely over recent decades. Understanding the role of jellyfish in the EBS ecosystem is required for fishery and ecosystem management; however, we lack direct measurements of the impact that changes in jellyfish biomass have had upon this ecosystem and its fish populations. We examined the role of jellyfish as competitors of juvenile forage fishes (herring and gadids) and juvenile salmonids by (1) examining the diets of the dominant scyphozoan jellyfish in the region, *Chrysaora melanaster*, and (2) estimating the dietary and spatial overlaps between jellyfish and major planktivorous pelagic fish taxa. Ocean sampling for diet analyses occurred in the summers of 2 contrasting years: 2014 (high jellyfish biomass, but only slightly above-average temperatures) and 2016 (low jellyfish biomass, anomalously high temperatures associated with a marine heatwave). Jellyfish diets primarily contained small copepods and pteropods and were generally more diverse, showing no significant overlap with the diet of small pelagic forage fishes, which consumed mainly euphausiids and other small fishes. Generally, jellyfish and small pelagic fishes showed low spatial overlap, but there was high spatial overlap between the small pelagic fish and salmonids, particularly in 2016. Spatial overlap and trophic interactions were not consistent throughout the EBS nor across years, although high overlap did occur between the species examined. These temporal variations in the degree of spatial overlap among zooplanktivores could result in resource competition in years or areas with low productivity or high jellyfish biomass.

KEY WORDS: Trophic interactions · Scyphomedusae · Planktivores · Stomach contents · Spatial variability · *Chrysaora melanaster*

1. INTRODUCTION

The eastern Bering Sea (EBS) shelf is a dynamic ecosystem, forced by a variable climate (Bond & Adams 2002, Eisner et al. 2014). Changes in ice conditions and timing of the spring bloom have been hypothesized to affect EBS zooplankton biomass (Hunt et al. 2011), and recent ecosystem studies have indicated that with cooling from 2006 to 2009, populations of large zooplankton (i.e. *Calanus marshallae*

and euphausiids) have increased (Coyle et al. 2011, Hunt et al. 2011). Temperatures in the EBS increased dramatically starting in 2014 related to a large-scale marine heatwave, known as the 'Warm Blob' (Bond et al. 2015), that affected much of the northeast Pacific at all trophic levels for several years (Di Lorenzo & Mantua 2016, Suryan et al. 2021). Anomalously high temperatures ($>2^{\circ}\text{C}$ above normal) altered the biomass and distribution patterns of many pelagic species in the EBS during this marine heatwave (Duffy-

*Corresponding author: marybeth.decker@yale.edu

Anderson et al. 2017, Yasumiishi et al. 2020, Oke et al. 2024). The ecosystem exhibited rapid responses to warming conditions in concert with reduced crustacean zooplankton biomass.

The highly productive EBS ecosystem supports large populations of jellyfish, including Scyphomedusae (primarily the northern sea nettle *Chrysaora melanaster*) and Hydromedusae, which have fluctuated substantially over the past 3 decades (Brodeur et al. 2008a, Decker et al. 2023). A steep increase in jellyfish biomass was documented over the EBS shelf throughout the 1990s (Brodeur et al. 2002). Biomass peaked in summer 2000 and then declined precipitously, stabilizing at a moderate level during 2001–2008. The onset of the biomass increase during the 1990s and decline in 2000 coincided with transitions between climatic regimes (Brodeur et al. 2008a). Peaks in zooplankton biomass during the time series preceded increases in jellyfish biomass, suggesting that food availability is a key factor contributing to fluctuations in Bering Sea jellyfish populations. Previous investigations of a 27 yr time series examining relationships between EBS jellyfish biomass and temperature, ice cover, atmospheric variables, current patterns, zooplankton biomass, and associated fish biomass indicated that jellyfish outbreaks during 1982–2004 were influenced regionally by interacting variables such as sea ice cover, sea surface temperature, currents, wind mixing, and prey availability (Brodeur et al. 2008a). A reanalysis of an updated time series up to 2017 showed that another peak in EBS jellyfish occurred from 2009 to 2015, followed by a precipitous decline the following years (Decker et al. 2023). Conversely, jellyfish respond negatively to increases in summer sea surface temperatures (Decker et al. 2023).

Due to their high abundance and spatial overlap (Brodeur et al. 1999, Cieciel et al. 2009, Decker et al. 2018) with some commercially important fish species in the Bering Sea, there is a potential for jellyfish, and especially *C. melanaster*, to negatively impact planktivorous fish through competition for limited prey resources. In other systems, the spatial distributions of jellyfish and early life stages of commercial fish and forage fish overlap significantly (Brodeur et al. 2008b, Eriksen et al. 2012). In Prince William Sound in the Gulf of Alaska, Purcell & Sturdevant (2001) found high spatial and trophic overlap between large jellyfish and pelagic fish and juvenile salmon, although the fish and jellyfish diets were sampled in different years. In the North Sea, Lynam et al. (2005) found negative relationships between jellyfish abundance and herring recruitment, indicating that jellyfish may

have negative impacts on commercial fisheries. Thus, in locations where jellyfish–fish overlap is high, predation by jellyfish on potential fish prey may be an important factor in the dynamics of commercially important fish species.

Jellyfish are important consumers of zooplankton and can significantly restructure food webs when their abundance is high (Kideys et al. 2005, Pitt et al. 2007). Field and modeling studies in the EBS and other ecosystems indicate that jellyfish can negatively impact fisheries because they compete with zooplanktivorous fish, feed on early life stages of fish, and indirectly compete with the other components of the food web by diverting plankton production away from upper trophic level consumers (Brodeur et al. 2008b, Ruzicka et al. 2012, 2016, 2020, Robinson et al. 2014, Opdal et al. 2019). The EBS is predicted to be an area where high jellyfish impact on forage fishes occurs, due to the high productivity of this system (Schnedler-Meyer et al. 2016). However, we lack an understanding of how EBS gelatinous predators affect energy flow through the ecosystem and how commercially important fish, specifically Pacific cod *Gadus macrocephalus*, walleye pollock *G. chalcogrammus*, Pacific herring *Clupea pallasii*, and juveniles of several abundant Pacific salmon species (*Oncorhynchus* spp.) may be impacted.

This study examines the overlap in distribution and feeding habits of jellyfish and fish, and among fish species in the southeastern Bering Sea during 2 distinct years with contrasting environmental conditions. The novelty of this research lies in its comparative approach, which allows for insights into how variable environmental factors (such as temperature and competition for prey resources) influence the interactions between these 2 groups. Jellyfish are often overlooked in ecosystem analyses (Pauly et al. 2009), yet they can have significant impacts on fish populations (Robinson et al. 2014, Ruzicka et al. 2020). By understanding when and where these overlaps occur, particularly under differing environmental conditions, the study can provide valuable information on how shifts in climate and ecosystem dynamics may affect fish populations in this region.

The overarching goal of this research was to estimate the levels of competition among forage fishes, juvenile salmon, and jellyfish in the EBS. To accomplish this, we examined the role of jellyfish as fish competitors by estimating their dietary and spatial overlap with pelagic planktivorous fish, including juvenile salmon, during years of high and low jellyfish abundance, and during years affected by a major mar-

ine heatwave. Also, we measured spatial and dietary overlap among the dominant planktivorous fishes to address potential competition within this feeding guild.

2. MATERIALS AND METHODS

2.1. Jellyfish and fish collection

Large medusae and juvenile fish were collected during National Marine Fisheries Service Alaska Fisheries Science Center (NMFS, AFSC) surveys in 2014 and 2016. Collections were made using a trawl net towed at the surface astern of the vessel during 18 August to 3 October 2014 and 23 August to 18 September 2016. The sampling grid covered the shelf off of western Alaska, from 160 to 168° W longitude and 55 to 59° N latitude (Fig. 1). Sampling extended across the 3 domains of the EBS shelf: inner (water depth 0–50 m), middle (water depth 50–100 m), and outer (water depth 100–180 m) (Schumacher & Stabeno 1998).

All trawling was conducted with a Cantrawl Pacific model 400/601 midwater rope trawl. The Cantrawl 400/601 trawl has hexagonal mesh in the wings and body, is 198 m in length, has a head-rope length of 120 m, and has a 12 mm mesh liner in the codend. The trawl was configured with 3 bridle legs (60 m long,

19 mm diameter) connecting the trawl to the trawl doors. Steel alloy 5 m² trawl doors with fixed bails from Nor'Eastern Trawl Systems were used to achieve horizontal spread. An additional 91 kg steel plate was added to the shoe of each door to increase stability. Three polyform floats (1 A-5, 2 A-3) were attached to the head-rope on both wingtips, and 1 A-3 polyform float was attached to the kite to help keep the headrope at the surface. A main warp of 350–400 m was targeted for consistency. Towing speeds ranged from 3.5 to 5.0 knots, depending on prevailing conditions.

Sampling effort was quantified as the area swept by the net at each station and was estimated as the product of horizontal opening and distance towed. On average, the horizontal spread of the net was 55 m (Farley et al. 2007). Distance towed was calculated as the haversine distance from the position of equilibrium (net deemed to be open and fishing) to haulback (the initial retrieval of the net). After each haul, fish were identified by species and life history stage (LHS). *Chrysaora melanaster* catch at each station was standardized to $\ln(\text{kg km}^{-2} + 1)$.

2.2. Environmental data

At each trawl station, water column oceanographic data were collected using Sea-Bird Electronics Model

25 conductivity–temperature–depth (CTD) sensors with a chlorophyll *a* fluorometer (Wet Labs Wet Star) calibrated with discrete chlorophyll *a* samples. Casts were made from the surface to 5–10 m above the bottom. For overall environmental conditions by cruise, temperature and chlorophyll *a* were averaged over the upper 10 m of the water column. To examine spatial patterns by station, temperatures were averaged over the upper mixed layer above the thermocline.

2.3. Gut content analysis

Specimens of the target jellyfish species *C. melanaster* were collected for gut analysis in the EBS (Fig. 1) from the surface at trawl stations with a long-handled dip-net to keep samples intact and to minimize net feeding. Specimens were collected to allow for diet

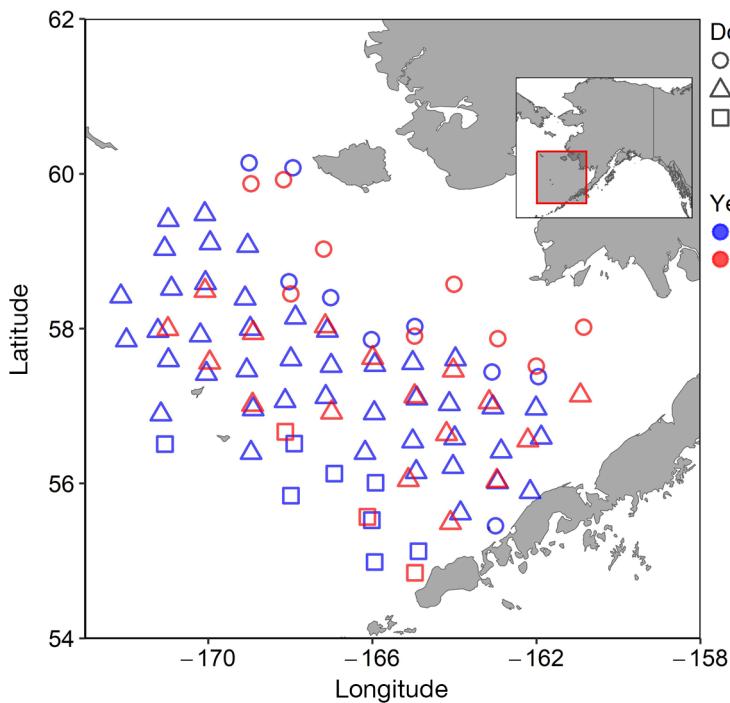


Fig. 1. Diet sampling stations in the eastern Bering Sea for each year

comparisons among medusae and pelagic fish. Upon collection, individual jellyfish were weighed and measured, and all gut and appendage contents were immediately preserved in 5% formalin in separate containers.

Gut content samples were also collected from the trawl for up to 10 fish per species/LHS identified as having potential overlap with *C. melanaster*, including Pacific cod, Pacific herring, walleye pollock, and juvenile pink *Oncorhynchus gorbuscha*, chum *O. keta*, sockeye *O. nerka*, and coho *O. kisutch* salmon. We limited our analysis to species that occurred at >2 stations per domain within a year. For the diet analysis, this resulted in 60 stations (9 in inner, 43 in middle, and 8 in outer domains) in 2014 and 29 stations (9 inner, 17 middle, 3 outer) in 2016.

For the fish samples, stomach contents were examined at sea. Stomach processing followed standard methods developed by Tikhookeanskiy Nauchno-Issledovatelskiy Institut Rybnogo Khozyaystva I Okeanografii (Chuchukalo & Volkov 1986, Moss et al. 2009, Coyle et al. 2011). Prey data for each fish species were pooled by collection to avoid pseudoreplication associated with sampling multiple individuals from the same trawl. For the fish diets, the stomach contents of up to 10 fish were combined and processed as a single sample at each station for each species. Contents were removed from the esophagus to the pylorus. Prey taxa (Table S1 in the Supplement at www.int-res.com/articles/suppl/m754p001_supp.pdf) were identified to the lowest possible taxonomic resolution using a dissecting microscope. Prey item composition and weight (± 1.0 mg) were recorded.

Jellyfish specimens were processed for diet content in the laboratory following standard methodological procedures (Suchman et al. 2008). Prey items in the gastric cavities, oral arms, and surrounding preservative medium were examined under a dissecting microscope and identified to the lowest taxonomic level possible and counted and/or weighed (± 1.0 mg). When only count data were recorded, average prey weights were used to convert count data to weight data prior to further analyses. For *C. melanaster*, we processed 41 gut content samples in 2014 and 64 gut content samples in 2016.

2.4. Data analyses

The spatial overlap among all taxa were estimated using the percent similarity index (PSI):

$$\text{PSI} = (1 - 0.5 \sum |P_{xi} - P_{yi}|) \times 100 \quad (1)$$

where P_{xi} corresponds to the relative proportion of the catch of species x in all trawls in a given year, and P_{yi} is the relative proportion of species y in the same survey.

To examine differences in temperature across years, we used a linear mixed-effects model (LMM) to account for both fixed and random effects in our data. Although we were primarily interested in 2014 and 2016, survey years 2004–2016 were utilized for this analysis, spanning multiple warm/cold periods. The LMM was implemented using the 'lmer' function in the R package 'lme4' (Bates et al. 2015), with year specified as a fixed effect and domain included as a random effect to account for spatial variability. The model equation was as follows:

$$\text{Temperature} \sim \text{Year} + (1|\text{Domain}) \quad (2)$$

Model fitting was performed using restricted maximum likelihood to obtain unbiased estimates of variance components. Degrees of freedom were estimated using the Kenward-Roger method, which is robust for models with unbalanced designs and small sample sizes.

To test the significance of the year effect on the response variable, we conducted an ANOVA on the fitted model. Since the ANOVA output did not provide p-values, we used a likelihood ratio test (LRT) to compare the full model (including Year as a fixed effect) with a reduced model (excluding Year). This approach allowed us to assess the significance of the Year effect through a chi-squared test on the difference in model deviance.

Following the overall significance test, we conducted pairwise comparisons of estimated marginal means between years using the 'emmeans' package (Lenth 2021). This allowed the direct comparison between 2014 and 2016. Pairwise contrasts were computed using the Tukey method to adjust p-values for multiple comparisons, controlling the family-wise error rate. This adjustment was essential to maintain a rigorous significance level, given the large number of yearly comparisons. For each contrast, we report the estimated difference in means (estimate), standard error (SE), t-ratio, and adjusted p-value.

All statistical temperature analyses were conducted in R (R Core Team 2023), and significance was set at $\alpha = 0.05$. Model assumptions were verified by plotting residuals vs. fitted values, a QQ plot for residuals, and a QQ plot for random effects.

To examine whether sea nettles and juvenile salmon and other pelagic fishes had different fine-scale spatial distribution patterns, we used the Cramér-von Mises non-parametric test (Syrjala 1996). The test accounts for spatial differences in population abun-

dance but is insensitive to the differences in abundance of each population. For the analysis, a single test statistic Ψ was calculated for each year between the catch per unit effort (CPUE) of sea nettles and all species of juvenile fishes. The test is calculated as the square of the differences between the cumulative distributions of the 2 groups, summed over all sampled stations, and it is sensitive to differences in the way groups are distributed across the study area regardless of differences in abundance. A p-value was computed based on 9999 random permutations of the data using the 'Syrjala' routine in the 'ecestpa' package (De la Cruz 2008) in the R programming language (R Core Team 2023).

Percent diet composition by weight was summarized by station and year for each species. Prey occurring in low numbers were pooled by major taxa categories. Dietary comparisons were made using PRIMER Version 7 (Anderson et al. 2008). All diet data were fourth-root transformed prior to statistical testing to give less weight to the most prevalent prey items prior to calculating similarity measures (Clarke & Warwick 2001). Assumptions of dietary variance homogeneity were tested using a permutation-based measure of variance (PERMDISP), which is analogous to a Levene's test for multivariate variances. Comparisons were made using either a mixed permutational multivariate ANOVA (PERMANOVA) design, or a 1-way ANOSIM operating on Bray-Curtis similarity matrices. PERMANOVA reports a pseudo- F statistic for global testing, and a t -value for pairwise testing, while ANOSIM reports a global R statistic, which is analogous to an ANOVA F statistic. Testing was completed for each year independently, among species within a domain. Species was treated as a fixed effect and domain was treated as a random effect. The preliminary analysis for 2014 found no significant interaction between species and domain, and the full PERMANOVA design was executed. The interaction between species and domain was significant for the

2016 period and the analysis was reduced to a 1-way ANOSIM by species for each domain within that year. Each of these models was fitted with type III sum of squares for its conservative approach and ability to handle unbalanced designs (Anderson et al. 2008). The SIMPER routine was used to identify prey categories that most influenced significant differences identified in the models above, as well as to provide an index of dietary overlap between each species within a domain and year. Non-metric multidimensional scaling (NMDS) ordination with bootstrapped means was used to visualize differences between study species within each year/domain combination. The farther apart 2 'clouds'/groups are on the NMDS plots, the greater the dissimilarity between the diets. Additionally, the larger the 'cloud', the more varied the diets are within a group. Species and domain combinations were only included in the analyses if they had been sampled at least 3 times within a year. Resulting sample sizes by year, species, and domain can be found in Table 1.

3. RESULTS

Our study was conducted during a warm period, which followed a cool period on the EBS shelf (Fig. S1). Overall surface layer temperature was 1.4°C warmer in 2016 (mean \pm SD = 12.67 \pm 1.81°C, n = 105) than in 2014 (11.27 \pm 1.32°C, n = 72; Fig. 2A) and the difference in model fit between the full and reduced models was significant (LRT, df = 11, χ^2 = 683.33, $p < 0.001$). This indicates that the full model provides a significantly better fit to the data than the reduced model (without year), suggesting that temperatures are significantly different between years. The pairwise comparison between 2014 and 2016 had an estimated effect of -1.31, suggesting that 2014 was cooler than 2016, and was significant (t -ratio = -5.78, df = 959, $p < 0.001$).

Table 1. Sample sizes of diet overlap by year, species, and domain on the eastern Bering Sea shelf

Domain	Sea nettle	Chum salmon	Coho salmon	Pink salmon	Sockeye salmon	Pacific cod	Pacific herring	Walleye pollock
2014								
Inner	0	4	0	0	5	0	5	6
Middle	4	0	0	0	25	8	10	40
Outer	3	0	0	0	0	4	0	6
2016								
Inner	4	6	0	0	5	0	0	3
Middle	6	6	0	10	15	0	4	14
Outer	0	0	0	3	3	0	0	0

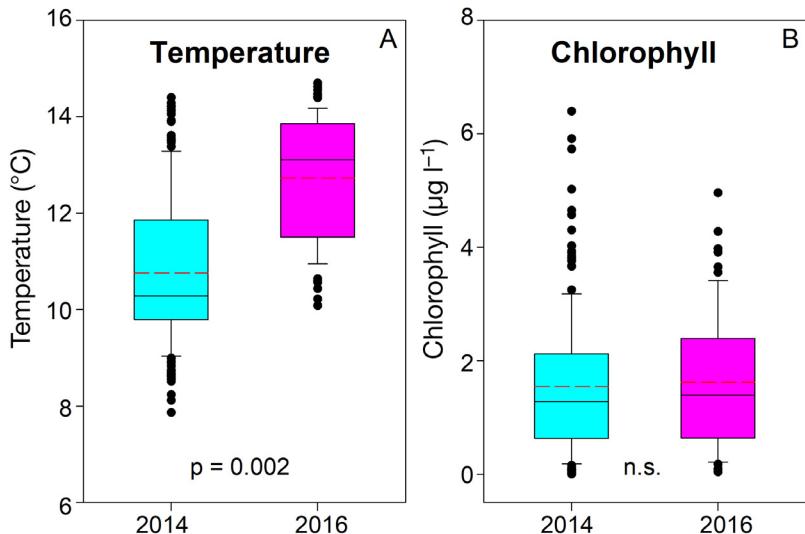


Fig. 2. (A) Temperature ($^{\circ}\text{C}$) and (B) chlorophyll ($\mu\text{g l}^{-1}$) values by station for the 2 years examined. Each value represents the mean of the upper 10 m values at each station (dashed line), the median value (solid line), the 75th and 25th percentiles (top and bottom of box), the 90th and 10th percentiles (upper and lower whiskers, respectively), and outlying values (points). Also shown are results of *t*-tests, which compared the means of temperature ($t_{174} = 9.42$, $p = 0.002$) and chlorophyll ($t_{174} = 0.44$, $p = 0.66$) measured in the 2 years

However, there were no significant differences ($t_{174} = 0.44$, $p = 0.66$) in surface chlorophyll between the 2 years (mean = 1.54 and 1.61, respectively; Fig. 2B). The spatial pattern of average surface layer temperatures by station reflected this difference, with 2016 showing areas of warm temperatures in northern

Bristol Bay and in the Middle Shelf Domain (Fig. 3).

Mean *Chrysaora melanaster* biomass was more than an order of magnitude higher in 2014 (1851 kg km^{-2}) than in 2016 (121 kg km^{-2}). Except for a few low catches in the Outer Shelf Domain, catches per station were uniformly higher in 2014, especially in the region near the Alaskan Peninsula (Fig. 4).

3.1. Jellyfish–fish spatial overlap

Sea nettles and small pelagic fishes generally had low spatial overlap in 2014, based upon the PSI values (Table 2). The highest PSI overlap values were for chum salmon with sockeye (43.9) and coho salmon (39.3). Coho salmon showed the only significant spatial overlap with sea nettles (25.1), and overall, this species exhibited the most (5 of 7 comparisons)

significant overlap based on the Cramér-von Mises tests (Table 2). By contrast, in 2016, there were some moderate to high spatial overlaps of sea nettles with walleye pollock (PSI = 60.0), coho (42.5), and sockeye (40.3) salmon (Table 3). The Cramér-von Mises test revealed that 5 of the 7 pelagic

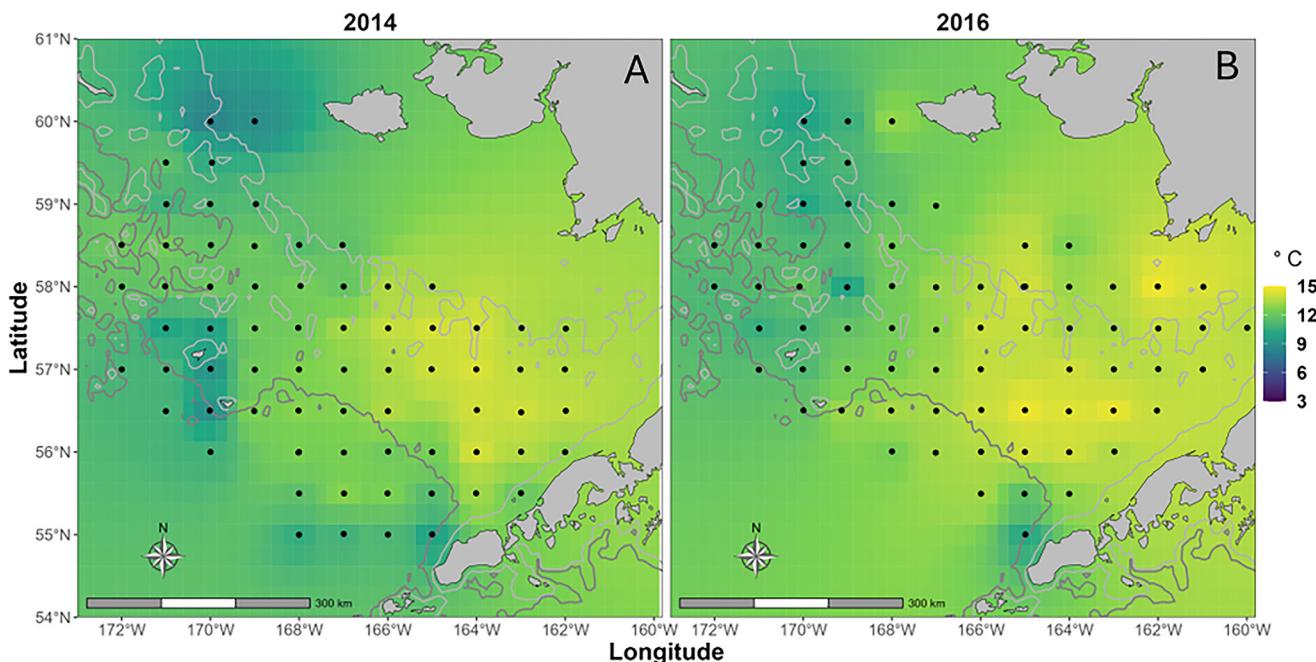


Fig. 3. Average temperature ($^{\circ}\text{C}$) measured in the upper 10 m in (A) 2014 and (B) 2016. Light gray contour: 50 m isobath; dark gray contour: 100 m isobath. Note that the area sampled in 2016 was less than in 2014

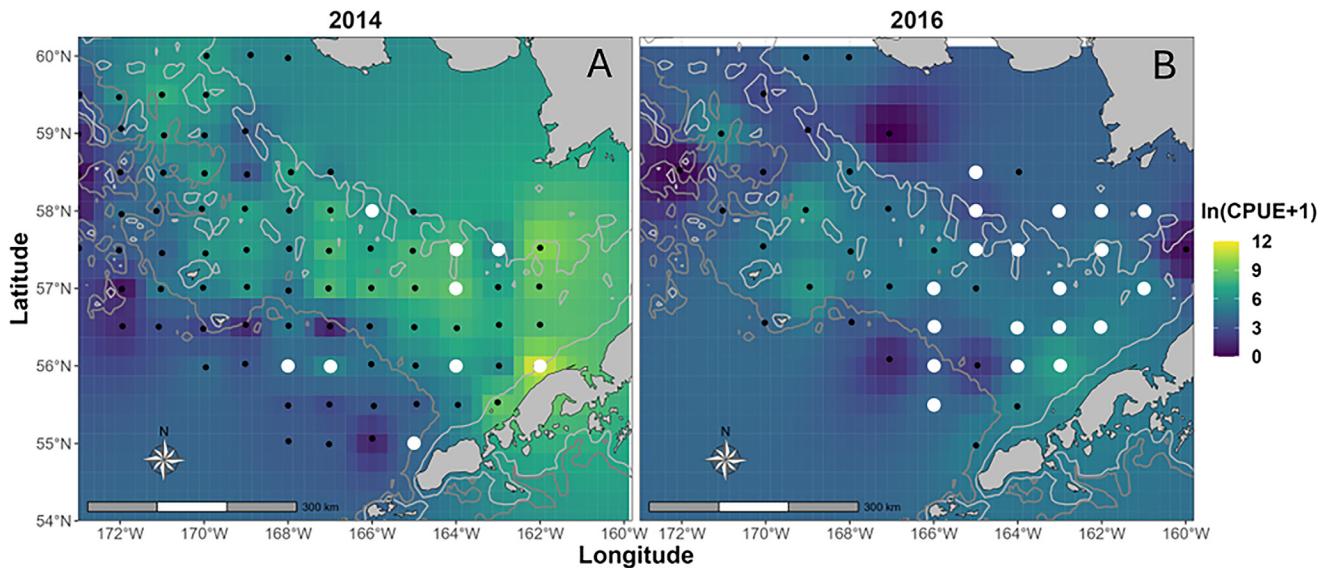


Fig. 4. *Chrysaora melanaster* standardized catch, measured as $\ln(\text{kg km}^{-2} + 1)$, per station in (A) 2014 and (B) 2016. Light gray contour: 50 m isobath; dark gray contour: 100 m isobath. White circles indicate locations of jellyfish diet samples

fishes (with the exception of coho and chum salmon) had significant spatial overlap with sea nettles in 2016 (Table 3). The overall majority of possible species spatial overlaps (16 of 28) were significant in 2016, in contrast to 2014, where only 6 of 28 were significant (Tables 2 & 3).

3.2. Jellyfish–fish diet overlap

C. melanaster diets were highly diverse in terms of major taxonomic groups consumed during both years (Fig. 5). Small copepods were an important prey item for *C. melanaster*, especially in 2016, while diets in 2014 contained appreciable amounts of chaetognaths and pteropods by weight. Age-0

walleye pollock were mostly zooplanktivorous, consuming primarily large copepods and euphausiids in both years (Fig. 5). By contrast, age-0 Pacific cod, Pacific herring, and all salmon species except pink salmon were mainly piscivorous, but often consumed euphausiids as secondary prey. Pink salmon consumed a variety of mostly crustacean prey, whereas chum salmon were the only predator that preyed upon gelatinous taxa (Fig. 5).

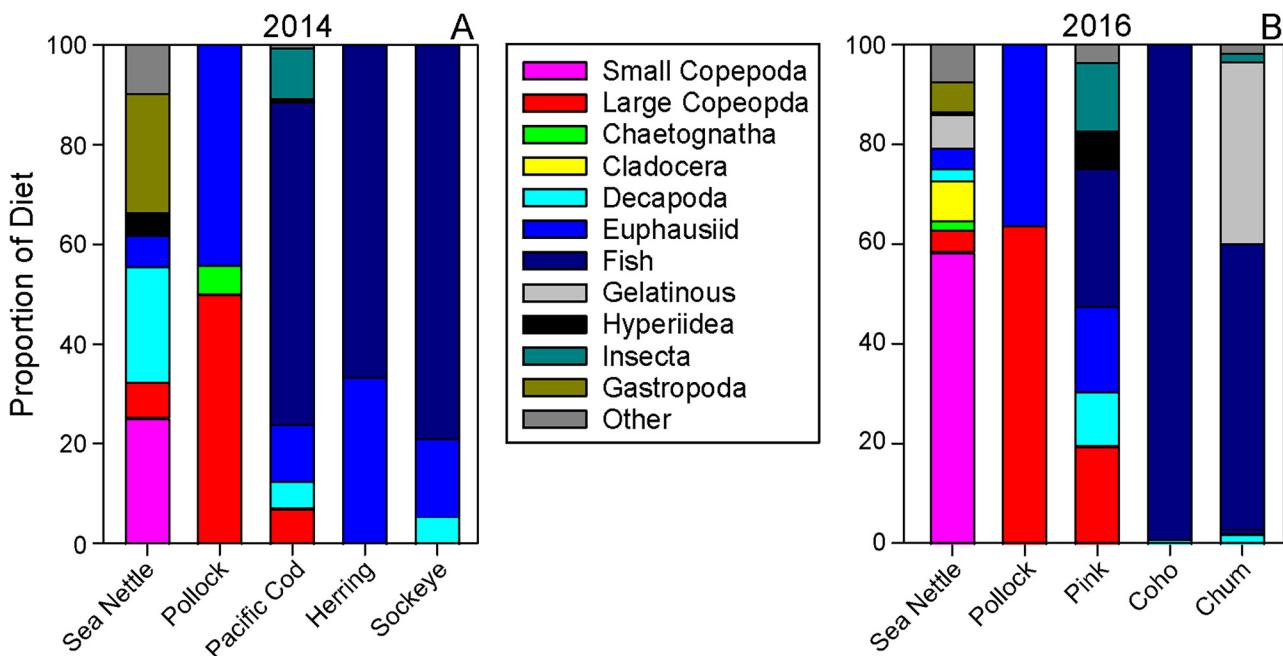
Overall, sea nettle diets differed significantly by domain and from diets of pelagic fish species in both 2014 (PERMANOVA: pseudo- $F_{\text{species}} = 8.5727$, $\text{df} = 5$, $p < 0.001$; pseudo- $F_{\text{domain}} = 3.8037$, $\text{df} = 2$, $p < 0.001$) and 2016 (ANOSIM, global $R = 0.406$, $\text{df} = 5$, $p < 0.001$). Pairwise tests showed that diet overlaps between species differed by domain and year.

Table 2. Spatial (percent similarity index, PSI; bottom of matrix) and diet (average similarity from SIMPER tests; top of matrix) overlap between *Chrysaora melanaster* and pelagic fishes during 2014. An 'X' indicates no diet samples available for overlap analysis. Pairs highlighted in bold are not significantly different ($p > 0.05$) based on Cramer-von-Mises tests (spatial pairs) or PERMANOVA tests (diet pairs)

	Sea nettle	Chum salmon	Coho salmon	Pink salmon	Sockeye salmon	Pacific cod	Pacific herring	Walleye pollock
Sea nettle	—	X	X	X	7.4	15.7	4.8	19.1
Chum salmon	30.7	—	X	X	32.5	X	26.0	12.9
Coho salmon	25.1	39.3	—	X	X	X	X	X
Pink salmon	14.0	17.3	18.9	—	X	X	X	X
Sockeye salmon	26.6	43.9	10.5	8.3	—	17.3	48.5	13.6
Pacific cod	36.5	10.3	7.5	6.1	5.6	—	18.7	27.9
Pacific herring	19.4	21.8	28.3	15.6	4.3	5.8	—	18.8
Walleye pollock	35.1	26.1	27.9	27.8	11.4	15.1	18.7	—

Table 3. As in Table 2, but for 2016

	Sea nettle	Chum salmon	Coho salmon	Pink salmon	Sockeye salmon	Pacific cod	Pacific herring	Walleye pollock
Sea nettle	—	3.0	X	4.1	3.8	X	7.5	10.5
Chum salmon	26.3	—	X	22.0	17.7	X	15.9	3.7
Coho salmon	42.5	41.9	—	X	X	X	X	X
Pink salmon	23.4	34.1	31.0	—	25.7	X	23.3	12.0
Sockeye salmon	40.3	32.4	45.4	37.1	—	X	20.9	9.2
Pacific cod	11.2	21.0	19.2	20.3	20.6	—	X	X
Pacific herring	30.7	23.2	27.1	10.1	10.3	25.9	—	26.4
Walleye pollock	60.0	20.8	40.6	18.3	42.9	9.5	35.5	—

Fig. 5. Percentage of main prey categories in sea nettle *Chrysaora melanaster* and pelagic fish diets by weight in (A) 2014 and (B) 2016

3.2.1. Jellyfish–fish diet overlap in 2014

No *C. melanaster* diet samples were collected from the inner domain in 2014 (Table 1). Therefore, we could not make comparisons with fish diets in the inner domain in 2014.

In the middle domain in 2014, sea nettle diets differed from all fish diets except Pacific cod (Fig. 6C; Tables S2 & S4). *Calanus* spp., *Limacina helicina*, euphausiids, cumaceans ('Other' category), and unidentified fish contributed 8–20% of the dissimilarity between the sea nettle and small pelagic fish diets (SIMPER analyses; Table S2). Sea nettles primarily consumed the pteropod *L. helicina* and cumaceans, while pelagic fish primarily consumed large calanoid copepods (*Calanus* spp.) and euphausiids (Fig. 5; Table S2).

In the outer domain in 2014, sea nettle diets differed from walleye pollock diets but not from Pacific cod diets (Fig. 6E; Tables S2 & S5). Euphausiids, *Cancer* spp., and *L. helicina* contributed 19–30% of the dissimilarity between the sea nettle and the walleye pollock diets (Table S2). The sea nettles primarily consumed *Cancer* spp. larvae and *L. helicina*, while walleye pollock exclusively consumed euphausiids (Table S2).

3.2.2. Jellyfish–fish diet overlap in 2016

In the inner domain during 2016, sea nettle diets differed from walleye pollock and chum and sockeye salmon diets (Fig. 6B; Tables S2 & S3). Here, small

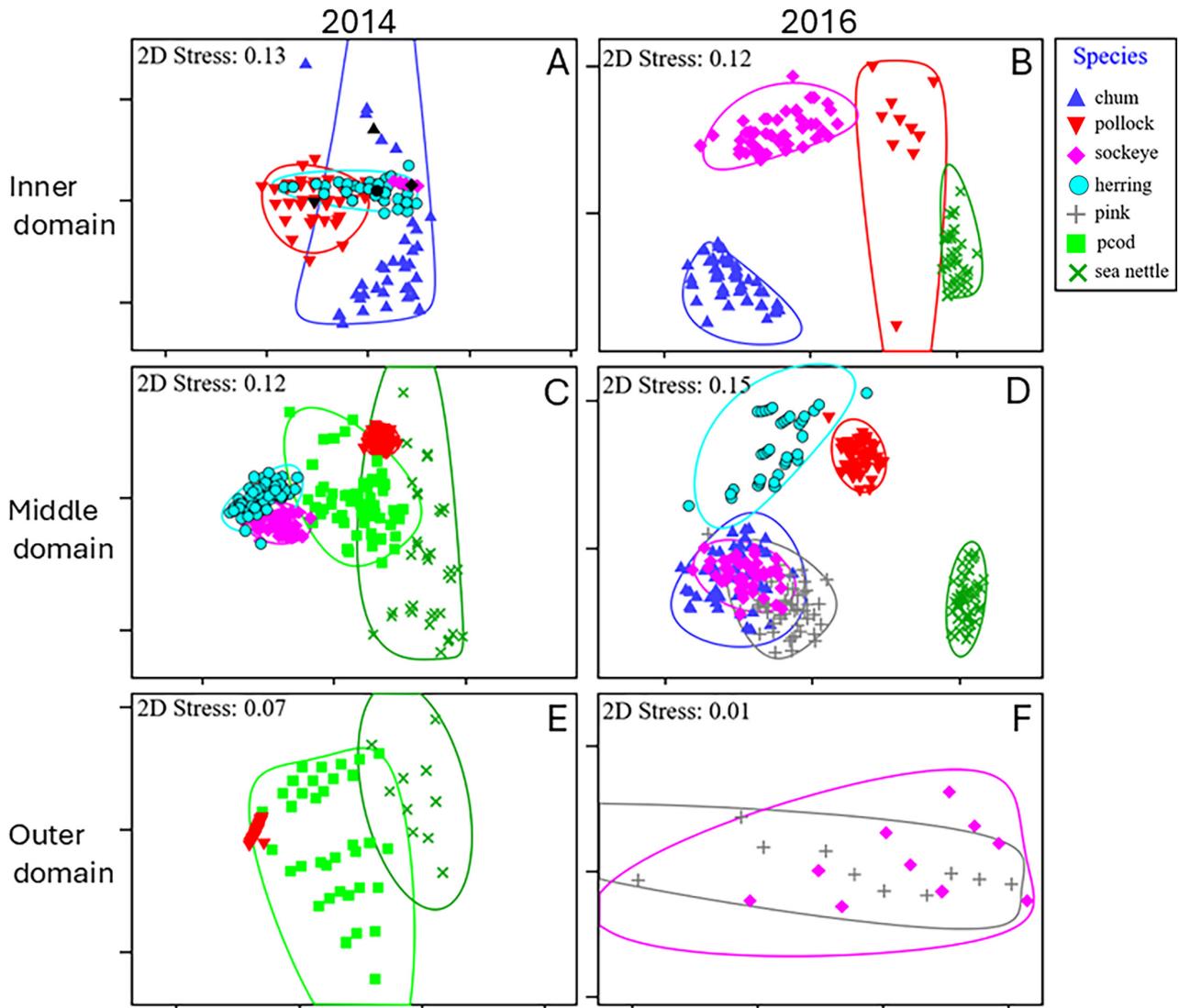


Fig. 6. Diet composition non-metric multidimensional scaling (nMDS) plots (bootstrap averages and nominal 95% regions) by year (columns), domain (rows), and species groups (symbols)

copepods, oikopleurans, and euphausiids contributed 6–14% of the dissimilarity between the sea nettle and the small pelagic fish diets (Table S2). The sea nettles primarily consumed small copepods (*Pseudocalanus* spp., *Centropages abdominalis*, *Acartia* spp., and *Oithona similis*) while the pelagic fish primarily consumed *Oikopleura* (chum salmon) and euphausiids (Table S2).

In the middle domain during 2016, sea nettle diets differed from chum, pink, and sockeye salmon, herring, and walleye pollock diets (Fig. 6D; Tables S2 & S4). Small copepods, brachyuran larvae, euphausiids, and fish (Gadidae and unidentified) contributed 9–19% of the dissimilarity between the sea nettle and the small pelagic fish diets (Table S2). The sea nettles exclusively consumed small copepods (*Pseudocala-*

nus spp., *C. abdominalis*, *O. similis*), while the pelagic fish primarily consumed Gadidae (herring and chum salmon), euphausiids, and general copepods (walleye pollock), and Brachyura larvae and unidentified fish (pink salmon) (Table S2).

No sea nettle samples were available for comparison in the outer domain in 2016 (Table 1).

3.3. Diet overlap among fish species

3.3.1. Pelagic fish diet overlap in 2014

In the inner domain during 2014, chum salmon diets differed from those of walleye pollock, sockeye, and herring (Fig. 6A; Tables S2 & S4).

Likewise, walleye pollock diets differed from sockeye salmon diets; however, no significant differences were observed between pollock and herring diets and sockeye salmon and herring diets (Fig. 6A; Tables S2 & S4). *Calanus* spp., *Epilabidocera amphitrites*, *Oikopleura* spp., euphausiids, Hyperiidae, and unidentified fish contributed 10–47% of the dissimilarity between the chum and sockeye salmon, pollock, and herring diets (Table S2). Chum salmon primarily consumed *Oikopleura* and some fish and unidentified prey; sockeye salmon and herring primarily consumed fish and unidentified prey; while walleye pollock primarily consumed large calanoid copepods, *Calanus* spp.

In the middle domain during 2014, walleye pollock diets differed from those of sockeye salmon, Pacific cod, and herring (Fig. 6C; Tables S2 & S4). Pacific herring differed only from Pacific cod, while Pacific cod only differed from sockeye salmon (Fig. 6C; Tables S2 & S4). Sockeye salmon and herring diets were not statistically different (Fig. 6C; Tables S2 & S4). *Calanus* spp., euphausiids, and unidentified fish contributed 14–32% of the dissimilarity between walleye pollock, Pacific cod, herring, and sockeye salmon (Table S2). Walleye pollock primarily consumed *Calanus* spp. and euphausiids, Pacific cod primarily consumed euphausiids, *Calanus* spp., and decapod larvae, and herring and sockeye salmon primarily consumed unidentified fish.

Walleye pollock and Pacific cod diets were significantly different in the outer domain in 2014 (Fig. 6E; Tables S2 & S5). Euphausiids and brachyurans contributed 24–29% of the dissimilarity between walleye pollock and Pacific cod diets (Table S2). Both fish species consumed euphausiids, but only Pacific cod consumed brachyurans (Table S2).

3.3.2. Pelagic fish diet overlap in 2016

In the inner domain in 2016, chum salmon diets differed from those of walleye pollock and sockeye salmon; however, walleye pollock diets were not statistically different from sockeye diets (Fig. 6B; Tables S2 & S3). *Calanus* spp., *C. abdominalis*, Chaetognatha, cnidarians, copepods, euphausiids, unidentified fish, and *Oikopleura* spp. contributed 8–17% of the dissimilarity between the chum and sockeye salmon and pollock diets (Table S2). Chum salmon consumed *Oikopleura* and unidentified fish, whereas sockeye salmon consumed unidentified fish and euphausiids. Walleye pollock consumed mysids and euphausiids.

In the middle domain in 2016, walleye pollock diets differed from diets of chum, pink, and sockeye salmon (Fig. 6D; Tables S2 & S4). Pacific herring diets differed from diets of pink and sockeye salmon; all other fish diet comparisons were not significantly different (Fig. 6D; Tables S2 & S4). Gadidae, euphausiids, copepods, brachyurans, and unidentified fish contributed 14–27% of the dissimilarity between chum, pink, and sockeye salmon, herring, and walleye pollock diets (Table S2). Chum, pink, and sockeye salmon consumed primarily Gadidae and brachyurans (chum and pink salmon), while herring and walleye pollock consumed primarily euphausiids (Table S2).

In the outer domain, the only samples available were juvenile pink and sockeye salmon (Fig. 6F). There was no difference between the dietary composition of the pink and sockeye salmon (pseudo- $F = 0.10$, $df = 1$, $p = 0.80$), which both consisted of euphausiids and brachyurans (Table S2).

4. DISCUSSION

The EBS experienced substantial warming during the 2 years of our study, due mainly to the widespread effects of the North Pacific marine heatwave which began in the Gulf of Alaska in 2014 and quickly spread throughout most of the basin including the Bering Sea (Bond et al. 2015, Suryan et al. 2021). Temperatures in the upper 10 m were highly anomalous and averaged several degrees warmer in 2014 and 2016 than any of the other years sampled during the NOAA pelagic fish survey dating back to 2002 (Yasumiishi et al. 2020). Although both years could be classified as extremely warm, we found greater differences in temperature between 2014 and 2016 than this longer-term study, which was based on a larger area extending up to the northern Bering Sea. Similarly, bottom temperature anomalies for the South-eastern Bering Sea were above average in 2014 but anomalously high in 2016, exceeding all previous years since the inception of the time series in 1995 (Spear et al. 2023).

Long-term observations of chlorophyll levels are not as prevalent as temperature records for the EBS. Lomas et al. (2020) showed that net primary productivity and phytoplankton growth rates were higher during our study period (2014–2016) compared to an earlier cold period (2007–2011), and chlorophyll concentrations were generally higher during the warmer period. Eisner et al. (2016) observed higher integrated chlorophyll levels in late

summer/early fall of warm years than in cold years in the southeastern Bering Sea. We did not find an interannual difference in chlorophyll levels, even though surface-layer temperature was warmer in 2016 than in 2014 (Fig. 2).

Differences in the availability and timing of primary production during warm and cold periods in the EBS have been hypothesized to be driven by sea-ice cover (Hunt et al. 2002, 2011) and related to changes in zooplankton biomass and species composition (Eisner et al. 2018, Kimmel et al. 2018), and recruitment of commercial fish (Duffy-Anderson et al. 2017). Reduced sea-ice cover in warm years results in low availability of large, lipid-rich *Calanus* species (Kimmel et al. 2018), emphasizing the potential influence of bottom-up control on competition among high trophic level organisms, such as the planktivorous jellyfish and fish in this study, for limited prey resources in this subarctic ecosystem.

The overall biomass of jellyfish in the survey trawls was an order of magnitude higher in 2014 than 2016, suggesting greater potential for competitive effects from *Chrysaora melanaster* in the earlier year. Based on a longer time-series of pelagic trawls, Yasumiishi et al. (unpubl.) found much higher densities of *C. melanaster* in 2014 than 2016, especially within our area of interest. These trends were consistent with the results from a broader-scale demersal trawl survey of the EBS that showed that jellyfish biomass was among the highest in 2014 and among the lowest in 2016 of the 40 yr time series (Decker et al. 2023).

Both pelagic fish and jellyfish distributions are likely to vary depending on ocean conditions, especially temperature. Elevated water temperatures have resulted in a poleward shift in demersal fishes and invertebrates (Mueter & Litzow 2008) and projected shifts in pelagic species (Cheung et al. 2015) in the Northeast Pacific. Northward shifts have been documented for many of the fish species examined in our study (Yasumiishi et al. 2020, Oke et al. 2024) as well as for *C. melanaster* (E. M. Yasumiishi unpubl.) during the marine heatwave of 2014–2016. Recent retreat of sea ice has allowed many of these species to inhabit arctic conditions in recent years (Levine et al. 2023), with jellyfish overlapping the distribution of all of the non-salmonids in our study in these high-latitude regions. In addition to horizontal distribution changes, pelagic fishes such as age-0 walleye pollock were distributed higher in the water column during the warm years of 2014 and 2016 compared to cooler years of 2011 and 2012 (Spear et al. 2023), which may further exacerbate the spatial overlap with surface-oriented jellyfish and juvenile salmon.

Previous examinations of spatial overlap between *C. melanaster* and forage fish in the EBS revealed that the degree of overlap varied inter-annually with fluctuations in jellyfish and forage fish biomass and with climate conditions on the shelf (Decker et al. 2018). Spatial overlap between jellyfish and age-0 walleye pollock was consistent throughout the study period (2004–2012), whereas the degree of jellyfish overlap with Pacific herring, age-0 Pacific cod, and capelin *Mallotus villosus* varied during warm and cool regimes when fish distributions changed in response to warming (Decker et al. 2018). Cieciel et al. (2009) also found substantial spatial overlap between several species of juvenile salmon and jellyfish, although this may be an artifact of the salmon migration through high jellyfish biomass areas.

Diet overlap between *C. melanaster* and the pelagic fishes was generally low during both years, and no significant overlaps were observed in our study (Tables 2 & 3, Fig. 6). In 2014, this species tended to have a more diverse array of prey than the co-occurring fish species, notably in the middle domain, and in both years consumed many smaller prey taxa not utilized by the fish (Figs. 5 & 6). This may be a result of a bias in sampling the relatively large juvenile fishes available at this time of the year. Overlap with jellyfish may be higher during the early spring and summer when the younger and smaller juvenile fishes present likely feed on mesozooplankton instead of fish.

Diet overlap between pelagic fishes was also generally low during both years, but significant overlaps were observed between some species, and occurrence of overlap was higher in 2016 (Tables 2 & 3, Fig. 6). Overall, diet variability was higher in 2014, indicating greater diversity in the prey being consumed. During shifts from warm to cool years in the Bering Sea, alterations in prey composition have been observed among the fish species examined here. Large juvenile walleye pollock predominantly consumed small juvenile pollock during warmer periods but transitioned to larger zooplankton during cooler conditions (Coyle et al. 2011). Small walleye pollock displayed a preference for small crustacean zooplankton in warm years, whereas in cooler years, they shifted towards consuming euphausiids and other large crustacean zooplankton (Coyle et al. 2011). Juvenile salmon exhibited similar patterns, primarily consuming juvenile pollock during warm years and switching to larger crustacean zooplankton during cooler periods (Andrews et al. 2009, Coyle et al. 2011). Dietary shifts have been observed in herring and capelin, with both species increasing their consump-

tion of large crustacean prey during colder years (Andrews et al. 2016). In warm periods, herring exhibited increased consumption of juvenile pollock while capelin retracted northward, with increased consumption of larvaceans. Juvenile Pacific cod shifted towards consuming primarily juvenile pollock during warm years and favored large crustacean zooplankton during cooler years in the middle domain (Farley et al. 2016). These observations collectively highlight the dynamic changes in prey selection among various species in the Bering Sea in response to shifts in temperature conditions.

In the context of environmental change, particularly in the Bering Sea, alterations in dietary overlap among fishes have been observed. The highest dietary overlap observed among salmon species in the Bering Sea occurred when and where prey abundance and diversity were at their lowest (Davis et al. 2009). These observations, taken in tandem with evidence of bottom-up control of production (Hunt et al. 2011, Kimmel et al. 2018), shed light upon the dietary interactions among these species. It is reasonable to assume that changing environmental conditions play an exaggerated role in shaping this dynamic. In addition, behavioral patterns and foraging strategy may also play a role in dietary overlap in the EBS. The low dietary overlap between capelin and juvenile pollock was assumed to stem from differing foraging strategies employed by these 2 species (Wilson et al. 2006). Capelin were thought to rely on mobility and prey patch dynamics, whereas age-0 pollock were more inclined toward prey switching as their primary strategy (Wilson et al. 2006). Additionally, it is worth noting that in the Gulf of Alaska, groundfish and salmon exhibited their highest dietary overlap during a cold year, specifically in 2012 (Daly et al. 2019). This observation suggests that prey resources were abundant and diverse enough to sustain pressure from multiple predator species (Daly et al. 2019). These observations highlight the relationships between environmental changes, prey availability, and the resulting dietary patterns among pelagic fish species. The variations in dietary overlap among species could be indicative of their adaptability and reliance on different foraging strategies in response to shifting environmental conditions.

During cool ocean conditions, jellyfish feed on large zooplankton, including *Calanus* spp. and euphausiids. Our study shows that *C. melanaster* diets contained fewer euphausiids than documented by Brodeur et al. (2002), and that they were feeding on small species of copepods and gastropods during the warm years of 2014 and 2016. Our data show that dur-

ing the warm years of 2014 and 2016, jellyfish were mainly feeding on small copepods (i.e. there were only a few large copepods and euphausiids in the diets), in contrast to walleye pollock, which consumed a lot of large copepods and euphausiids (Fig. 5). When large zooplankton are abundant during cool periods, jellyfish diets contain copepods and euphausiids (Brodeur et al. 2002). While that may mean diet overlap by our metrics would be high, if prey are not limiting, competition would be weak. By contrast, during very warm conditions, pollock are selecting the larger zooplankton to feed upon, but the jellyfish are feeding on small copepods, and few euphausiids (Fig. 5). Under these conditions, we expect diet overlap and competition to be low, as we observed in this study (Fig. 6). However, we predict that the strongest competition between jellyfish and pollock may occur during average temperature conditions, when large zooplankton are present, but not in abundance (Coyle et al. 2011, Hunt et al. 2011).

Understanding food competition among fish species in the southeastern Bering Sea is crucial due to the complex and dynamic ecosystem of the region. Multiple fish species rely on overlapping food sources, such as zooplankton and small fish, leading to competition that can influence growth rates, reproductive success, and survival, thereby affecting population dynamics and species abundance (Coyle et al. 2011, Hunt et al. 2011, Strasburger et al. 2014). Environmental changes, including shifts in sea temperature, ice cover, and prey availability, further alter resource distribution and availability, intensifying this competition (Coyle et al. 2011).

Given that many of these fish species support commercial fisheries, understanding their competitive interactions is essential for developing sustainable management strategies. By identifying key factors driving food competition, fisheries managers can better predict potential shifts in fish stocks, enabling proactive adjustments to quotas and protections that align with ecosystem-based management practices. This understanding is also vital for anticipating the impacts of climate change, as altered competitive dynamics could lead to cascading effects throughout the food web, affecting not only the fish themselves but also the predators and human communities that depend on them. These studies provide a foundation for understanding the complexities of food competition among fish species in the southeastern Bering Sea and the importance of informed management practices in the face of environmental change.

The effects of *C. melanaster* on pelagic fish extend beyond the potential for competition. Firstly, this spe-

cies has been shown to consume an estimated 2.8% of the standing stocks of juvenile walleye pollock daily around the Pribilof Islands (Brodeur et al. 2002). Although not specifically identified to species, fish eggs and larvae were found in the diet of *C. melanaster* sampled in the present study (Decker et al. unpubl. data). Walleye pollock are the dominant (~94% of total caught) larval and juvenile fish taxon caught in the central Bering Sea during summer (Duffy-Anderson et al. 2006, Oke et al. 2024), so it is likely that these unidentified eggs and larvae were this species. Pacific cod have demersal eggs, herring are inshore spawners, and salmon reproduce in estuarine and freshwater systems, so it is unlikely that early life stages of any of these species would be consumed by jellyfish in pelagic waters over the shelf. In other ways, the presence of jellyfish can be somewhat beneficial to fishes. Juveniles of some species, such as walleye pollock, were found to be living commensally within the tentacles of *Chrysaora*, potentially providing shelter from predation (Brodeur 1998, Sato et al. 2015). Moreover, several demersal fish species including walleye pollock consume Scyphozoa, albeit at low levels compared to other prey taxa (Brodeur et al. 2021).

The potential benefits of this research extend to fisheries management and conservation efforts. By identifying how environmental changes impact the competition between jellyfish and fish, and within fish, fisheries managers can better predict shifts in fish stock health and the relationship to jellyfish biomass and distribution, which can inform more resilient management strategies. This study also contributes to broader ecosystem-based management approaches by highlighting the role of jellyfish as both competitors and ecological indicators in marine ecosystems (Richardson et al. 2009).

5. CONCLUSIONS

Spatial and trophic overlaps among jellyfish and fish were generally low during 2014 and 2016, during which conditions on the EBS shelf were anomalously warm. However, regions of high overlap among jellyfish and fish do occur, which could result in resource competition among planktivores in years or areas of low to moderate availability of preferred fish prey (i.e. large calanoid copepods and euphausiids). High overlap in space and diet does not necessarily suggest that competition is occurring, unless shared prey resources are limiting during these high overlap periods. However, a high biomass of *Chrysaora fus-*

cescens has been shown to impact juvenile salmon feeding and apparent survival in the Northern California Current (Ruzicka et al. 2016) and to reduce the production of fish and higher trophic-level consumers on the EBS shelf (Ruzicka et al. 2020).

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