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ORIGINAL ARTICLE

Abundance, composition and distribution of carnivorous gelatinous zooplankton in the Northern Gulf of Alaska

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Abundance, biomass, size and distribution of macro-jellyfish were measured in the Northern Gulf of Alaska (NGA). Nearly 1000 kg dispersed among ∼13 800 jellyfish were collected using a 5-m^2 Methot net. We present length-weight regressions for seven most-common taxa. Catches were dominated by the hydrozoan *Aequorea victoria* and the scyphozoan *Chrysaora melanaster*. During 2018, epipelagic macro-jellyfish biomass averaged 1.46 ± 0.36 g WW m^{-3} for July and 1.14 ± 0.23 g WW m^{-3} for September, while during 2019 they averaged 0.86 ± 0.19 g WW m^{-3} for July and 0.72 ± 0.21 g WW m^{-3} by September. Despite similar biomass among seasons within a year, July abundances were fivefold greater than abundances in September, with July catches dominated by smaller-sized jellyfish over the inner shelf, while during September larger jellyfish were more prominent and most predominant at offshore stations. Comparison to 20 years of data from standard towed nets allowed determination of the relative magnitude of the dominant carnivorous zooplankton components: scyphozoans, hydrozoans and chaetognaths in the NGA. The biomass of these smaller epipelagic predators (5.4 mg WW m^{-3} for hydrozoans and 10.5 mg WW m^{-3} for chaetognaths) is a low percentage of the macro-jellyfish, despite their much higher numerical abundance.

KEYWORDS: jellyfish; biomass; abundance; Gulf of Alaska; fisheries

INTRODUCTION

Jellyfish are among the most conspicuous components of the zooplankton communities and long recognized as being voracious predators. Nonetheless, what they eat, and their true role within the food web has been elusive until recently. Gut content and stable isotope analyses confirm many eat a variety of other zooplankton and that their diet can overlap substantially with those of forage fish species (e.g. Purcell and Sturdevant, 2001; Brodeur *et al*., 2002; Purcell, 2003). Even for large species such as *Chrysaora melanaster* in the Bering Sea, diet analysis shows they mostly consume pteropods, chaetognaths and gelatinous zooplankton, with the crustacean meso- and macro-zooplankton making up just 10–50% of their diet by weight (Ruzicka *et al*., 2020).

Historically, jellyfish have been incorrectly seen as trophic dead-ends (Verity and Smetacek, 1996; Richardson *et al*., 2009; Chiaverano *et al*., 2018), while forage fish have been viewed as the critical trophic link between zooplankton and higher trophic levels, such as vertebrate consumers (Purcell and Sturdevant, 2001). Competition between jellyfish and forage fish is important because, in locations where they overlap, jellyfish can negatively impact fisheries by preying competitively upon zooplankton, as well as by directly consuming fish eggs and larvae (Decker *et al*., 2018). In places where their abundance is high, jellyfish can out-compete fish populations because jellyfish can have higher feeding rates, and because they can respond more rapidly to pulses of food than their competitors (Brodeur *et al*., 2002; Flynn *et al*., 2012). To place this in context, *Chrysaora* has a fivefold greater impact on ecosystem resources on the mid-shelf of the eastern Bering Sea than seabirds, marine mammals and marine fisheries combined (Ruzicka *et al*., 2020). Given this predatory potential, a global debate is currently underway focused on whether anthropogenic stressors have led to increased jellyfish blooms with dire consequences, or if such concerns have been amplified beyond the data-driven evidence (Condon *et al*., 2012, 2013; Pitt *et al*., 2018).

In Alaskan waters, multi-decadal observational datasets exist for large jellyfish in the Bering Sea (Brodeur *et al*., 2008; Decker *et al*., 2023) but are short in the Gulf of Alaska (GoA) (Zador and Yasumiishi, 2018). These surveys were designed primarily to assess populations of commercially important demersal fish and invertebrates using gear that is minimally efficient for sampling within the water column (i.e. bottom trawls are not fully open during ascent and descent), hence these biannual surveys greatly underestimate the abundance for large jellyfish (Rooper, 2017). A third observation set using near-surface rope trawls was performed along the eastern GoA from 2011 to 2017 (Cieciel and Yasumiishi, 2018), but quantitative estimates of jellyfish biomass are hampered by variable mesh sizes from the net mouth to the cod end of their trawls. Hence, large-sized gelatinous zooplankton biomass remains poorly quantified in Alaskan waters, although it has been suggested that their biomass is greatest within the Bering Sea (Ruzicka *et al*., 2020).

Traditional oceanographic methods poorly sample many gelatinous taxa (Haddock, 2004; Purcell *et al*., 2010; Brotz *et al*., 2012), yet several multi-decadal Alaskan time-series do provide reasonable quantitative estimates for some smaller soft-bodied taxa amenable to capture using the nets routinely deployed in the assessment of zooplankton and larval fish. The biomass of the hydromedusa *Aglantha digitale*, and the chaetognaths *Parasagitta elegans* and *Eukrohnia hamata* can be important in the GoA (Coyle and Pinchuk, 2003, 2005), the Bering Sea (Coyle *et al*., 1996) or even further north (Questel *et al*., 2013; Ershova *et al*., 2015; Smoot and Hopcroft, 2017). These two groups differ greatly in their feeding style, with jellyfish being encounter predators, while chaetognaths are selective ambush predators capable of targeting specific prey. Like the larger macro-jellyfish, both small hydromedusae and chaetognaths are often considered potential predators of larval fish (Feigenbaum, 1991), yet their predatory role on fish larvae versus copepods remains uncertain (Baier and Purcell, 1997; Brodeur and Terazaki, 1999). At present, we lack robust data on the comparative importance of meso- and macro-jellyfish in Alaskan waters, but particularly so in the GoA.

Changes in gelatinous zooplankton biomass may affect fisheries, thus it is essential to understand and quantify the role of various gelatinous groups in the food web (Han and Uye, 2009; Purcell, 2009; Robinson *et al*., 2014). As a first step, we sought to quantify the biomass of the macro-jellyfish (i.e. those large but rare taxa poorly quantified by traditional sampling techniques) in the Northern Gulf of Alaska (NGA), and compare their biomass to that of the better-known smaller gelatinous carnivores (i.e. hydrozoans and chaetognaths). We hope this will provide a clearer view of the trophic role of these gelatinous carnivores, and thereby lead to improved management of marine ecosystems (Decker *et al*., 2018; Ruzicka *et al*., 2020).

METHODS

The GoA is characterized by energetic storm systems and massive runoff (∼24 000 m^3 s^{-1}) that discharge a critical source of iron to the primary production on the GoA shelf ecosystem (Royer, 1982; Coyle *et al*., 2012). The shelf is influenced by two major current systems, the Alaska Coastal Current, a westward-flowing buoyancy-driven current along the coast (∼50 km wide) and the Alaskan Stream, a westward-flowing buoyancy-driven current near the shelf break (Weingartner, 2007). These currents and their interaction with the coastal topography transport mesoscale eddies that influence cross-shelf mixing of the water masses (Okkonen *et al.*, 2003; Coyle *et al.*, 2012). Mixing of iron-poor, nitrate-rich basin water with iron-rich, nitrate-poor coastal water promotes elevated productivity on the shelf, particularly during summer and fall (Coyle *et al.*, 2013, 2019) when the system is stratified with a mixed layer depth of 15–30 m (Danielson *et al.*, 2022).

The abundance, biomass, size and distribution of large gelatinous zooplankton were determined during July and September of 2018 and 2019 as part of the Northern Gulf of Alaska Long-Term Ecological Research (NGA-LTER) cruises. For simplification, throughout the study we are referring to the July survey as "summer" sampling and the September survey as "autumn" sampling, although the September cruise straddled both the end of summer and the beginning of autumn. Surveys were performed along three or four cross-shelf transects in the NGA and within western Prince William Sound (PWS). Samples were collected from just below the surface (i.e. 0–3 m) using a 5 m^2 Methot net (Methot, 1986) made of knotless-netting with 3×5 mm openings, towed at 2.5–3 knots for 20 min (i.e. ∼6600 m^3 filtered per tow) during night-time or occasionally during dawn or dusk. The volume filtered was estimated using a calibrated General Oceanics flowmeter placed in the middle of the net mouth. All gelatinous taxa were identified, counted, bell diameter (or length) measured, and wet-weight (WW) was determined to the nearest millimeter and gram, respectively. When catches were large, diameter and weight measurements were performed on a subsample of at least 30 individuals each tow. Jellyfish biovolume is strongly correlated to diameter and wet-weight, hence, volume was also recorded for some species to account for potential errors in weight when sea state was high, as well as to estimate the total catch per species when bodies were highly fragmented. Total wet-weight of each taxa was always measured directly at each station.

As a consequence of the coarse mesh and towing speed, many soft-bodies tax were extruded through our net. We thus restricted our analysis to species with firm mesoglea and bell diameters (or lengths) typically exceeding 1–2 cm and ignored the typically low catches of smaller and/or less robust hydrozoan taxa (e.g. *A. digitale*, *Eirene indicans*, *Clytia* sp.), most ctenophore species and thaliaceans that we considered to be collected non-quantitatively. The only ctenophore amenable to this collection methodology was *Hormiphora palmata*, so it was included in our analysis, but for simplicity we include it within our macro-jellyfish umbrella despite its taxonomic affinity. Some field identifications remain problematic, and while we have confirmed most identifications through sequencing (e.g. *Aurelia labiata;* Lawley *et al.*, 2021), *Cyanea capillata* should be considered provisional. To place our data in perspective, we compared our Methot catch to those of smaller cnidarians and chaetognaths from the Seward Line time series (1998–2019) that were collected quantitatively at night-time using 505-μm Midi-Multinets or 1 m^2 MOCNESS that typically sampled ∼100 m^{-3} for each of five nets deployed in 20 m strata within the upper 100 m (see Coyle and Pinchuk, 2003, 2005; Sousa *et al.*, 2016). Variance was calculated from annual means of the 13 stations sampled per cruise. Means and variance at 60–80 and 80–100 m do not include 2018 or 2019 because these two strata were combined after 2017.

The Methot data were standardized to number per 1000 m^3 for macro-jellyfish and biomass per cubic meter for all taxa. Using the length-weight relationships determined by this study, and assuming that observations in summer and autumn capture the same cohorts, sizes changes between the smaller size mode in summer and larger size mode in autumn were used to calculate instantaneous growth rates for each species (Runge and Roff, 2000).

Preliminary analyses and visualization were done using MATLAB 2017a and SigmaPlot 11.2. Maps were prepared using ArcGIS 10.6. Analysis of Variance (ANOVA) or *t*-tests with a $(\log + 1)$ transformation was employed to test for differences between cruises. Bray–Curtis resemblance was determined for 4th root transformed data that was employed for hierarchical clustering and non-parametric Multidimensional scaling (nMDS) using Primer7. Relationships to environmental variables (surface temperature, surface salinity, bottom depth and onshelf/offshelf location) and the Bray–Curtis similarity matrix were examined for abundance and biomass with the distance-based linear model (DistLM) routine using the Best selection option and marginal tests (with 9999 permutations) performed with Primer 7, alpha of 0.05 was considered for all *P*-values. Physical data were taken from Seabird Electronics SBE 911 temperature/salinity (CTD) profiles provided by the NGA-LTER program (Danielson and Dobbins, 2023).

RESULTS

A total of 966 kg dispersed among 13 782 jellyfish was caught from a total of 138 collections during the four sampling expeditions (Table I). During 2018, macro-jellyfish biomass averaged 1.46 ± 0.36 g WW m^{-3} for

Table I: Biomass and abundance of jellyfish caught and average volume sampled per collection during the different sampling seasons in the NGA. P-values determined by ANOVA

Sampling Season	Avg. Volume (m^3)	Total n. Jellyfish	Abundance (ind. 1000 m^{-3})	STD (± ind. 1000 m^{-3})	*P*-value Abundance	Jellyfish (Kg)	Biomass (g m^{-3})	STD (± g m^{-3})	*P*-value Biomass	Total n. Stations	*P*-value Biomass	*P*-value Abundance
Summer 2018	6169	5974	26	0.022	*$P < 0.001$*	334	1.46	0.307	$P = 0.627$	37		
Autumn 2018	6671	1228	4.5	0.004		311	1.14	0.274		41	$P = 0.154$	$P = 0.158$
Summer 2019	6208	5563	24	0.017	*$P = 0.034$*	198	0.86	0.195	$P = 0.535$	37		
Autumn 2019	7399	1017	6.0	0.004		123	0.72	0.192		23		

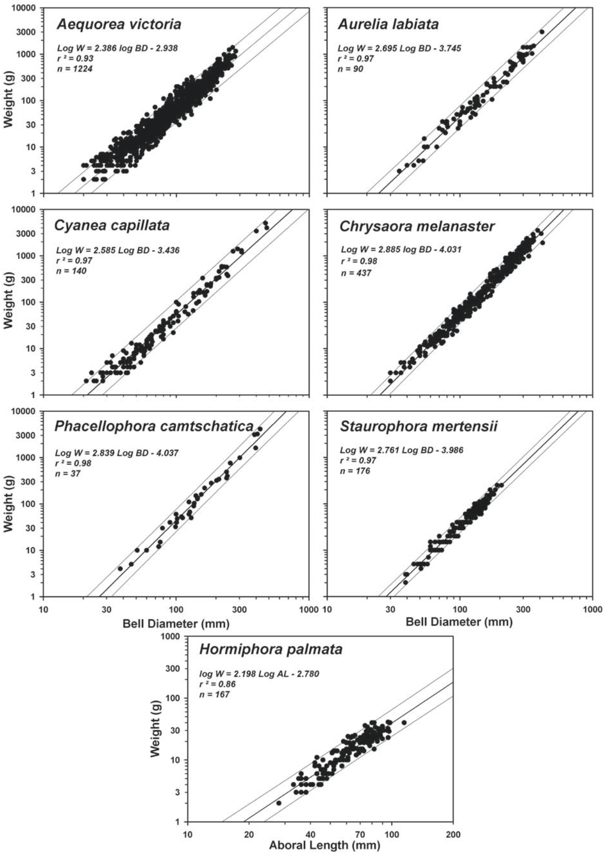

Fig. 1. Relationship between wet-weight (g) and bell diameter (mm) of larger gelatinous zooplankton in the NGA. The 95% prediction intervals bracket each regression line. Data from 2018 and 2019 have been augmented with measurements from more recent years for the less common species.

July and 1.14 ± 0.23 g WW m^{-3} for September and were not significantly different. The abundance in July was five times greater than September, 5974 and 1228 individuals, respectively, representing 26 and 4.5 individuals per 1000 m^{-3}, respectively ($P = 0.001$). The 2019 sampling averaged 0.86 ± 0.19 g WW m^{-3} through July and 0.72 ± 0.21 g WW m^{-3} by September with no significant difference. Once again, abundance in July was fivefold greater than September, 5563 and 1017 individuals representing 24 and 6.0 indiv. 1000 m^{-3}, respectively ($P = 0.034$). Biomass and abundance values between matching months for the 2 years were not statistically significant.

Strong relationships between bell diameter (or aboral length) and wet-weight were observed for our seven prominent species (Fig. 1). Most regressions were based on over 100 measurements, yet even with a limited number of individuals and a wide range of sizes, the scyphozoan *Phacellophora camtschatica* produced a strong regression ($r^2 = 0.97$). A slightly lower regression coefficient for the ctenophore *H. palmata* ($r^2 = 0.86$) arose due to a more limited size range.

The Methot catches were dominated by two macro-jellyfish, the hydrozoan *Aequorea victoria* and the scyphozoan *C. melanaster* (Table II). *Aequorea* was present at most stations, making up to 90% of the total abundance in most surveys. During July 2018, the *Aequorea* contribution averaged 1.04 g WW m^{-3} and by September 2018, 0.66 g WW m^{-3} biomass per station, although these differences were not significant. Abundance was 23.8 indiv. 1000 m^{-3} during July and dropped to 3.7 indiv. 1000 m^{-3} during September 2018 ($P = 0.008$). Throughout July of the following year, *Aequorea* biomass averaged 0.49 g WW m^{-3} and 0.53 g WW m^{-3} during September, and abundance averaged 21.6 and 5.3 indiv. 1000 m^{-3} for July and September, respectively (Fig. 2), neither of which were significantly different. During July and September, *Chrysaora* ranked second in terms of abundance and biomass, with an average biomass per station of 0.38 g WW m^{-3} for July 2018 and a similar 0.30 g WW m^{-3} for September 2018. Corresponding abundance of 1.12 and 0.32 indiv. 1000 m^{-3} during July and September 2018, respectively, were significantly different ($P = 0.019$). During 2019, *Chrysaora* biomass was 0.34 and 0.15 g WW m^{-3} and abundance was 1.34 and 0.47 indiv. 1000 m^{-3} for July and September, respectively (Fig. 3), but these differences were not significant (Table II).

During September 2018 *A. labiata* mean biomass (0.09 g WW m^{-3}) was higher ($P = 0.002$) than during July (0.005 g WW m^{-3}) particularly for the outer-shelf stations, the highest abundance was recorded during July 2019 (0.68 indiv. 1000 m^{-3}) at the inner-shelf stations. In terms of macro-jellyfish biomass, *Aurelia* ranked third on most cruises with the exception of July 2018 when it was displaced by *H. palmata* (0.02 g WW m^{-3}). *Hormiphora* was present only during 2018 cruises. The abundance of *Hormiphora* during September 2018 (0.29 indiv. 1000 m^{-3}) was similar to abundance of *Chrysaora* (0.32 indiv. per 1000 m^{-3}), but the biomass of *Hormiphora* was lowest (0.004 g WW m^{-3}) because of its small body-size relative to the rest of the macro-jellyfish caught (Table II).

Significant differences in biomass between years for the same seasons were not observed for our taxa with the exception of *Aurelia* ($P = 0.01$) and *Hormiphora* ($P = 0.008$) during both July and September. Biomass of the scyphozoan *Cyanea* was similar among July 2018 and both 2019 cruises (0.018, 0.014 and 0.016 g WW m^{-3}, respectively), but was nearly double (0.03 g WW m^{-3}) during September of 2018, although not significantly so, whereas abundance was different between seasons for 2018 ($P = 0.029$). As with *Aurelia*, *Cyanea* showed higher biomass along the offshore stations throughout September 2018 (Fig. 4).

Table II: Biomass (g WW m^{-3}) and abundance (jellyfish 1000 m^{-3}) of all macro-jellyfish caught during the different sampling cruises. Differences determined with paired tests after log transformation for season within year (S) and season between years (Y): $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

	Biomass (g WW m^{-3})							Abundance (1000 m^{-3})						
	Summer 2018	S	Autumn 2018	Y	Summer 2019	S	Autumn 2019	Summer 2018	S	Autumn 2018	Y	Summer 2019	S	Autumn 2019
Aequorea victoria	1.04		0.66		0.49		0.53	23.81	**	3.67		21.66		5.34
Chrysaora melanaster	0.38		0.30		0.34		0.15	1.12	*	0.32		1.34		0.47
Aurelia labiata	0.005	**	0.09		0.015		0.02	0.076		0.15	*	0.68		0.065
Cyanea capillata	0.018		0.03		0.014		0.016	0.18	*	0.04		0.49		0.10
Hormiphora palmata	0.02	**	0.004					0.96		0.29				
Staurophora mertensii	0.002				0.003			0.024				0.026		
Phallcellophora camtschatica			0.05		0.005					0.022		0.017		
Ptychogena lactea	0.00004							0.004						

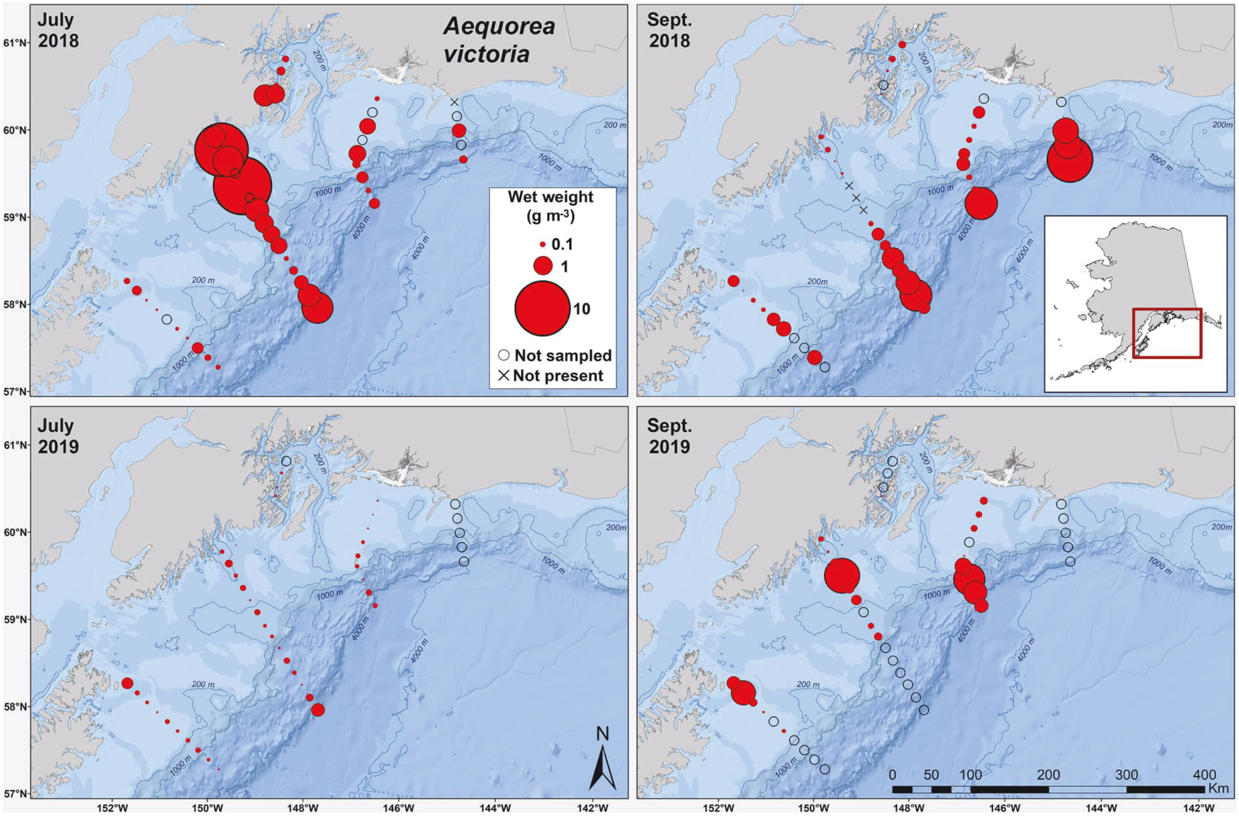

Fig. 2. *Aequorea victoria* distribution and biomass (g WW m^{-3}) in the NGA. Upper panels are 2018 sampling cruises and bottom panels are 2019 sampling cruises.

Only 12 individuals in total of the hydrozoan *Staurophora mertensii* were collected during July of both years, and only on the continental shelf (0.002 and 0.003 g WW m^{-3}; 0.024 and 0.026 indiv. 1000 m^{-3}, for 2018 and 2019, respectively). Even more rarely found was the scyphozoan *P. camtschatica* with six (0.022 indiv. 1000 m^{-3}) caught during 2018 and four individuals (0.017 indiv. 1000 m^{-3}) caught during 2019, all along stations located across the shelf break. Only a single individual of the hydrozoan *Ptychogena lactea* (0.004 indiv. 1000 m^{-3}) was captured, near Kodiak Island during the July cruise 2018 (Table II).

Consistent shifts in cross-shelf and size distributions were observed between summer and autumn 2018. Higher abundance occurred at inner shelf sampling stations, where catches were dominated by smaller jellyfish within each taxon, while catches in the outer-shelf stations were lower in number but of greater size (e.g. *Chrysaora* and *Aequorea*; Fig. 5). During summer sampling, the hydrozoan *Aequorea* and the scyphozoans *Aurelia*, *Chrysaora* and *Cyanea* showed higher abundance of smaller individuals among nearshore stations. An exception occurred for *Chrysaora* that showed two peaks (small and large) during summer. In contrast, during autumn large jellyfish were more prominent and most predominant at offshore stations. Our estimations for instantaneous growth rate in *Aequorea* was 0.03 d^{-1}, for *Chrysaora* it was 0.06 d^{-1}, for *Cyanea* it was 0.04 d^{-1}, and for *Aurelia* it was 0.03 d^{-1}. Size changes for *Hormiphora* differed from cnidarians, with most specimens being of larger size during summer sampling, while a wider range of sizes occurred during fall.

There were five major clusters in the macro-jellyfish species at 60% similarity, although permutation test did not consider any of the clusters significant. When projected spatially, there was no clear pattern within or among cruises, aside from a general patchiness where nearby stations often clustered into small groups and those clusters could occur across multiple cruises (Fig. 6). Both biomass and abundance (not shown) clustering produced very similar spatial projections. nMDS also failed to produce significant or interpretable patterns.

Including all taxa, the average abundances for July 2018 were 44 and 10 indiv. 1000 m^{-3} in the inner- and outer-shelf stations, respectively ($P = 0.074$), and by September 2018, the average abundances were six and 20 indiv. 1000 m^{-3} along the inner- and outer-shelf stations, respectively ($P < 0.0001$). During 2019, jellyfish abundances were more evenly distributed

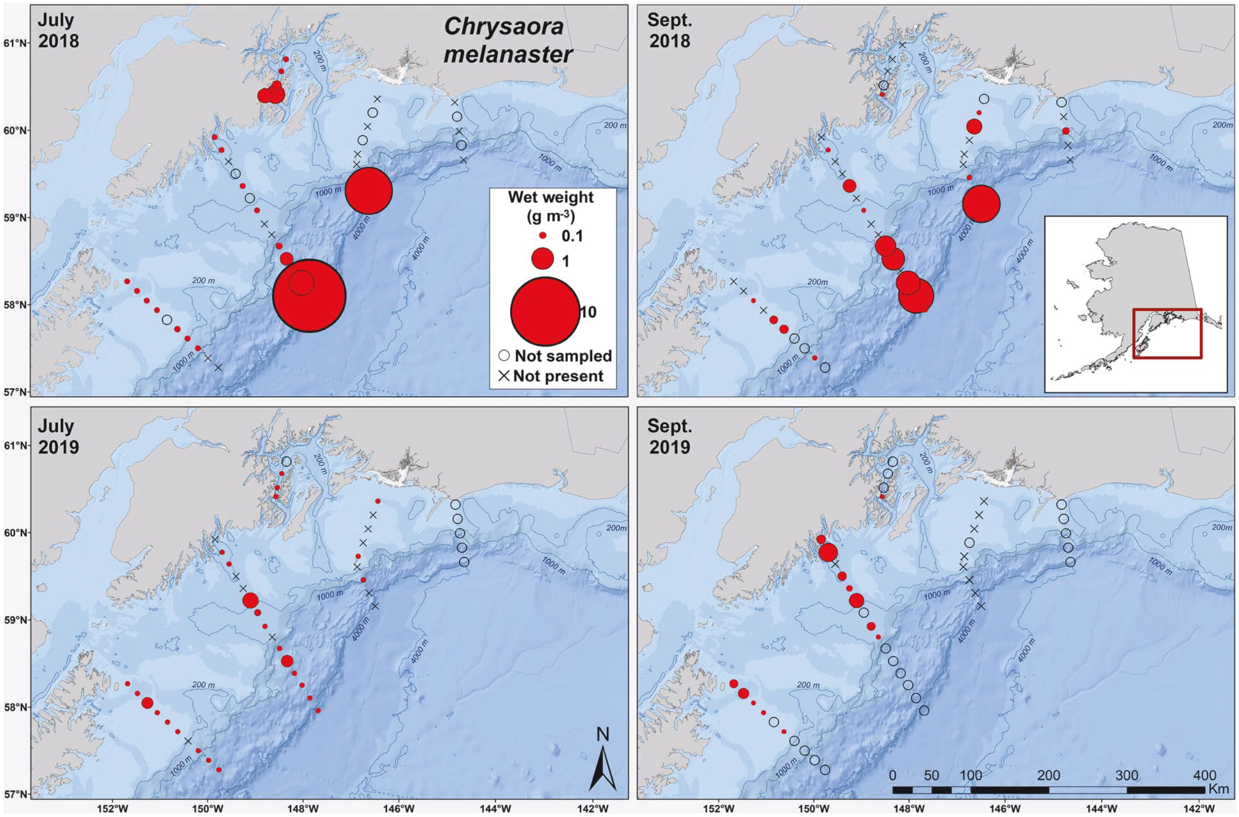

Fig. 3. *Chrysaora melanaster* distribution and biomass (g WW m^{-3}) in the NGA. Upper panels are 2018 sampling cruises and bottom panels are 2019 sampling cruises.

along the shelf. July 2019 abundances averaged 24 and 21 indiv. 1000 m^{-3} for in- and offshore stations, respectively ($P = 0.72$). September 2019 abundances averaged six and seven indiv. 1000 m^{-3} for in- and offshore stations, respectively ($P = 0.83$); these non-significant differences might be a consequence of limited offshore sampling imposed by autumn storm systems.

Differences in macro-jellyfish distribution on shelf and beyond the shelf break were supported by DistLM analysis (Fig. 7). With the full dataset, biomass showed a clear separation of the data by in- and offshore stations (all data pooled in the same analysis), finding significant differences between the jellyfish biomass related to bottom depth ($P < 0.001$) and surface salinity ($P < 0.001$), but no relationship to surface temperature ($P = 0.126$), albeit with a weak coefficient of determination ($R^2 = 0.09$). Splitting biomass by season, DistLM analysis for summer cruises identified bottom depth ($P = 0.015$), but not surface salinity ($P = 0.224$) or surface temperature ($P = 0.355$), while for autumn cruises bottom depth ($P < 0.001$), surface salinity ($P < 0.001$) and surface temperature ($P = 0.049$) were all influential. Although the seasonal environmental variables showed significant differences, their coefficients of determination to macro-jellyfish were weak ($R^2 = 0.08$ and $R^2 = 0.25$, respectively, for each season). Similarly, DistLM analysis for abundance showed a clear separation of the data by in- and offshore stations. Once again, salinity was significant ($P = 0.003$), while bottom depth and surface temperature were not (0.069 and 0.07, respectively). Splitting the data by season, summer sampling showed no significance for surface salinity ($P = 0.124$) or temperature ($P = 0.283$) but significance for bottom depth ($P = 0.008$), but with weak coefficient of determination ($R^2 = 0.09$). Contrastingly, abundance during autumn sampling showed significant influence of salinity ($P = 0.011$) and depth ($P < 0.001$), but no significance for surface temperature ($P = 0.055$), with a low coefficient of determination ($R^2 = 0.2$).

For comparison, the total biomass of smaller hydrozoan jellyfish and chaetognaths combined along the Seward Line was at least 10 times lower than the biomass of the macro-jellyfish (Fig. 8). The biomass of small jellyfish averaged 5.8 and 5.1 mg WW m^{-3} across the upper 100 m during May and September, respectively, and was dominated by the trachymedusan *A. digitale* and the leptothecatan *E. indicans*. The biomass of chaetognaths averaged 12.3 and 8.8 mg WW m^{-3} across

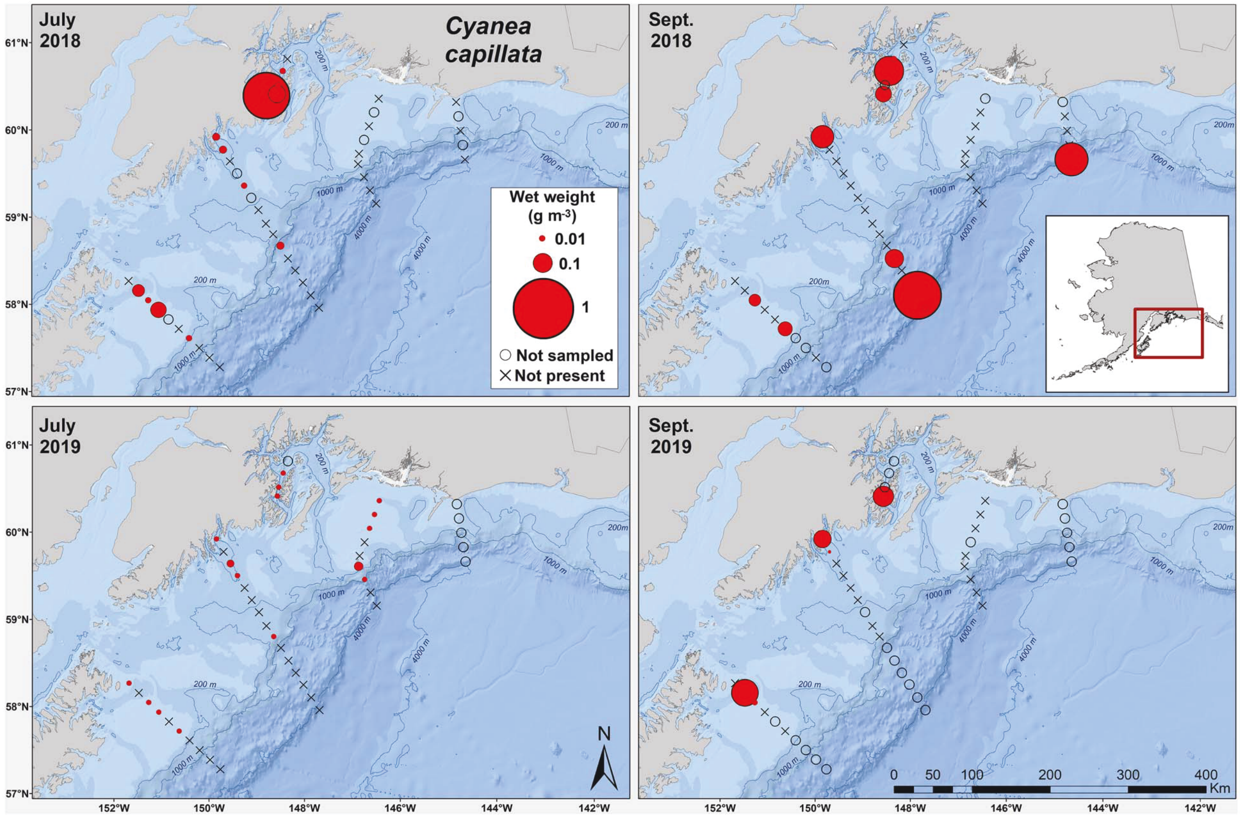

Fig. 4. *Cyanea capillata* distribution and biomass (g WW m^{-3}) in the NGA. Upper panels are 2018 sampling cruises and bottom panels are 2019 sampling cruises.

the upper 100 m during May and September, respectively, split relatively evenly between *P. elegans* and *E. hamata* during spring, but dominated (90%) by *P. elegans* during September (Fig. 7). Notably, the biomass of *P. elegans* was 4–5-fold greater within the mixed layer than below it, while *E. hamata* was more evenly spread throughout the water column. *Pseudosagitta scrippsae* contributed 5–10% of the chaetognath biomass in both seasons and was spread evenly throughout the upper 100 m. All showed considerable inter-annual variability, with 2018 and 2019 being generally typical years within the 20-year time series. In the case of *Aglantha*, animals found within the mixed layer were 5–10 times greater in biomass than at depth during both May and September. *Eirene indicans* had similar preference for the mixed layer but was nearly absent during May and sometimes comparable in biomass to *Aglantha* during September.

DISCUSSION

Large gelatinous zooplankton have been poorly documented in Alaskan waters. Most of the available records of macro-jellyfish in the GoA have come as a byproduct of fisheries assessments (e.g. where gear differences most certainly affect their catch rates; Rooper, 2017). Although quantitative estimates exist for the nearby PWS, where biomass can become extremely aggregated and exceed 1 g WW m^{-3} (Purcell, 2003), the present study is the first quantitative report of the major carnivorous gelatinous zooplankton in the surface waters of the NGA shelf and offshore waters. This work has quantified the high biomass (~1 g WW m^{-3}) and the low absolute abundance (~25 indiv. 1000 m^{-3}) of macro-jellyfish in surface waters of the NGA, that even exceed those reported for PWS (Purcell, 2003). Additionally, we have established for the first time the comparative magnitude of the three dominant gelatinous carnivorous zooplankton components: scyphozoans, hydrozoans and chaetognaths. The biomass of these smaller carnivores (i.e. 5.4 mg WW m^{-3} for hydrozoans and 10.6 mg WW m^{-3} for chaetognaths, across the upper 100 m) is a low percentage of the macro-jellyfish, despite their much higher abundance, reflecting the vast difference in size among these taxonomic groups.

Somewhat surprisingly, we could not determine clear spatial or temporal patterns to community composition

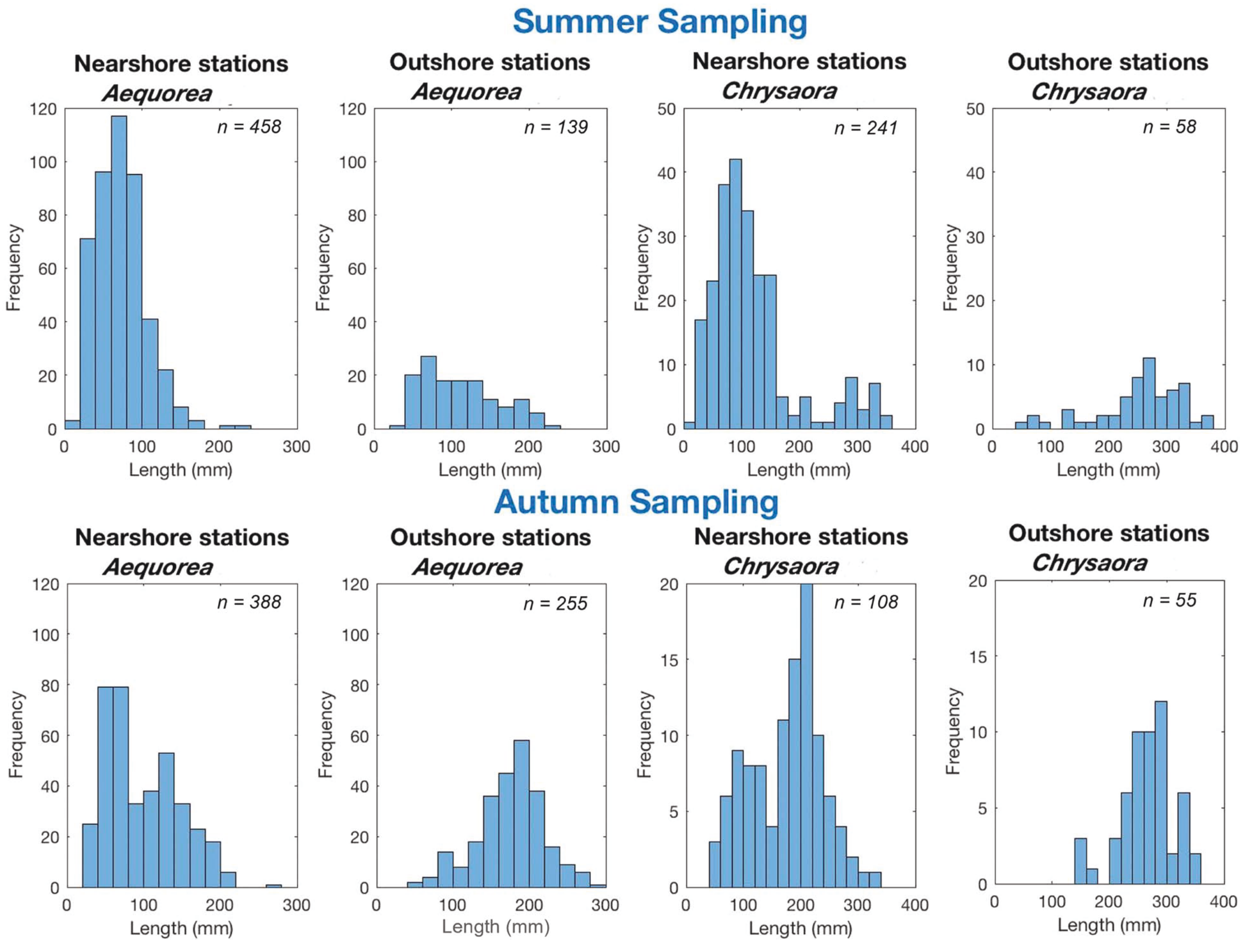

Fig. 5. *Aequorea* and *Chrysaora* size frequency distribution histograms plotted by season and sampling location (near- and offshore) stations in the NGA. *Aequorea* autumn sampling is based on 2018 data (limited size data were recorded for the second year of sampling).

either abundance or biomass, although some overall patchiness was suggested, a character common to most local satellite imagery (Coyle *et al.*, 2012). Several environmental variables were implicated as being significant, however their overall explanatory power was very weak. It is possible or even likely that apparent correlations to temperature and salinity were simply capturing the typically saltier character of offshore waters, while the temperature correlation was reflecting differences in the stratification mechanisms of inshore and offshore waters (Sarkar, 2007) rather than true environmental preferences.

Life cycle and cross-shelf patterns

The high productivity of large-bodied zooplankton that support high macro-jelly biomass in the Bering Sea (e.g. Ruzicka *et al.*, 2020), also favors these species in the NGA. Nonetheless in Alaskan waters these carnivores' pelagic life phase must be timed to take advantage of the spring and summer productivity in this highly seasonal environment. We propose the reproductive biology of the cnidarians, and the GoA circulation patterns interact to create the observed seasonal cross-shelf distribution. The production of medusae takes place seasonally, often in the spring (Purcell, 2005; Sigurdsson *et al.*, 2021), from an asexual benthic stage—the scyphistoma in Scyphozoa, or a hydroid in the Hydrozoa. These polyps arise from the settlement of larvae produced by the pelagic medusoid sexual stage (Purcell, 2005; Purcell *et al.*, 2007). Indeed, most of the available records of wild polyp distribution come from harbors located within embayments (Miyake *et al.*, 2002; Ishii and Katsukoshi, 2010; Toyokawa *et al.*, 2011). For the NGA, we believe this benthic stage is probably most common on hard substrate close to the coast, hence smaller jellyfish appear near the coast during summer and by autumn they have grown into adult jellyfish and dispersed further away from the shore. Inability to

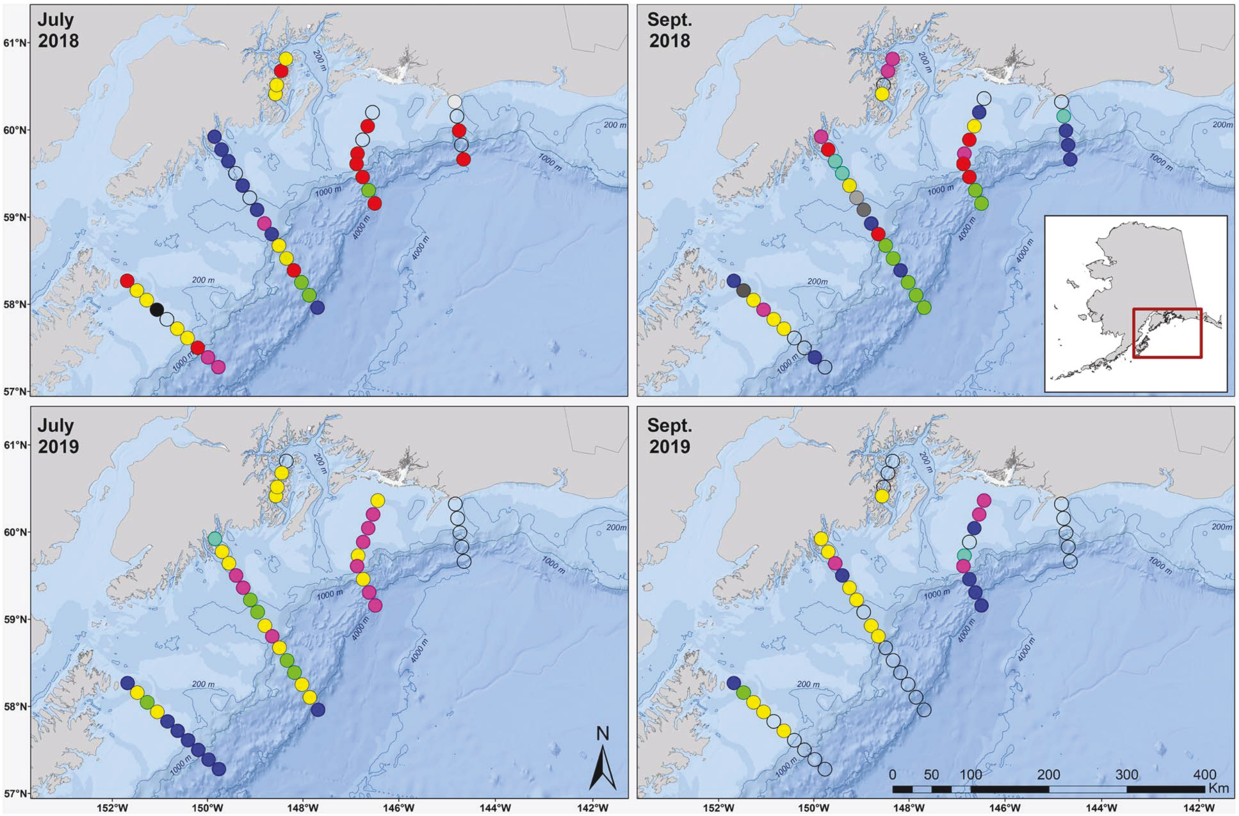

Fig. 6. Hierarchical clustering of Bray–Curtis similarity using macro-jellyfish biomass from the NGA. Clustering was performed using samples aggregated across cruises, with color groups reflecting 60%.

sample at most offshore stations during September 2019 hampered our ability to confirm this as typical.

The GoA is an energetic environment, with strong tidal currents and subtidal flows (Weingartner *et al.*, 2005; Stabeno *et al.*, 2016) that carry water and the entrained plankton from east to west. The offshore jellyfish populations probably originated at inshore stations to the east of our sampling domain weeks to months earlier. We propose that various cross-shelf exchange mechanisms (Mackas and Coyle, 2005) move these jellyfish offshore, where the food environment remains favorable and predation upon them could be reduced, although intraguild predation there could be significant (Purcell, 1991). Furthermore, as the season progresses the shelf environment becomes more dominated by smaller crustacean zooplankton compared to offshore waters (Coyle and Pinchuk, 2003, 2005) potentially creating a more challenging feeding environment for jellyfish. Thus, the jellyfish reproductive biology, the circulation patterns and food environment could interact to produce lower scyphozoan biomass near shore and larger biomass offshore during autumn in some years.

Ctenophores did not show any seasonal pattern of abundance, nor size distribution, possibly related to their holopelagic nature. Ctenophores lack a benthic stage, are hermaphroditic and reproduce by the fusion of eggs and sperm in the water column (Purcell, 2005; Purcell *et al.*, 2007). Most catches of *H. palmata* were of the larger body size during summer (i.e. likely adults), while a wider range of sizes observed during autumn suggested the ongoing recruitment. Smaller (<3 cm) *H. palmata* were seldom observed but a smaller spherical *Hormiphora* species (1–2 cm) — frequently misidentified as *Pleurobranchia bachei* in the NGA — was excluded because they were less robust and not quantitatively sampled due to extrusion through the mesh. Nonetheless, several other more fragile ctenophore species known to occur in the NGA (e.g. *Bolinopsis infundibulum*, *Beroe* spp., *Thalassocalyce* sp., *Dryadora glandiformis*) are also not well-represented in either of the nets reported here, and remain a potential target for future assessment using optical approaches (e.g. Luo *et al.*, 2014; Treible *et al.*, 2022).

Allometries and growth rates

An important aspect of our study was the establishment of robust length-weight relationship for our dominant

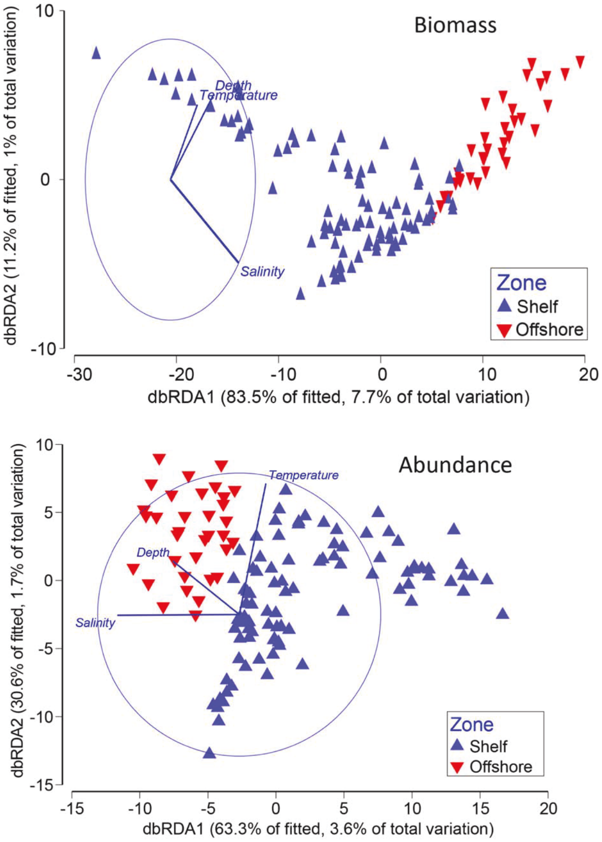

Fig. 7. Relationship between macro-jellyfish assemblages and environmental variables in the GoA as indicted by DistLM.

species. These relationships agree well in their slope to those published for common, broadly distributed genera (e.g. *Aurelia, Chyrsaora, Cyanea*) except for cases where the number of observations was limited and slopes appear suspect (Supplement Table 1). In contrast, for four genera (*Aequorea, Phacellophora, Staurophora, Hormiphora*) where size-mass relationships are not well established, such relationships are of more fundamental utility.

Although admittedly crude, estimations for instantaneous growth rate for *Aequorea* (0.03 d^{-1}), *Chrysaora* (0.06 d^{-1}), *Cyanea* (0.04 d^{-1}) and *Aurelia* (0.03 d^{-1}) were comparable to other studies from similar temperatures. *In situ* observations for *Aequorea vitrina* estimated growth ranges from 0.02 to 0.05 d^{-1} (Møller and Riisgård, 2007), while for *Aurelia aurita* with specific growth rates of 0.09 d^{-1} (Olesen *et al*., 1994), 0.069 d^{-1} (Uye and Shimauchi, 2005) and 0.05–0.17 d^{-1} (Møller and Riisgård, 2007) have been reported. Under laboratory-controlled conditions and unlimited food, *A. aurita* reached a maximum growth rate of 0.022 d^{-1} (Olesen *et al*., 1994), which is unexpectedly lower than our and many other *in situ* observations. More recently, 0.06 d^{-1} has been determined for laboratory reared *Aurelia* sp. (Riisgård and Larson, 2022). Moreover, all of these rates are several times lower than GoA copepod growth rates, which range upward to 0.285 d^{-1}, while increasing progressively from March to October (Liu and Hopcroft, 2006, 2008). Copepod production estimated from daily growth rates for the NGA averages ∼35 mg C m^{-2} day^{-1} annually, and is concentrated within the mixed layer and over the continental shelf where it can sustain a mean production over 100 mg C m^{-3} during August–October (Coyle *et al*., 2013, 2019). Although individual macro-jellyfish may be consuming thousands of copepods per day in the GoA (Purcell *et al*., 2003), their abundances are relatively low, while their carbon content per unit WW is only 0.2–2% (McConville *et al*., 2017; Lüskow *et al*., 2021). This suggests a macro-jellyfish carbon biomass of ∼10 mg C m^{-3}, requires $<$1 mg C m^{-3} to sustain it. Thus, the higher growth rates, higher carbon content and high abundance of copepods makes them a suitably sustainable food resource for these gelatinous zooplankton and helps account for the large difference in wet-weight biomass between them and their gelatinous predators.

Vertical distribution

An unresolved aspect of the patterns we observed are the potential biases introduced by our sampling methodology. If most jellyfish are evenly distributed throughout the mixed layer (as appears to be the case for our smaller jellyfish; see also McClatchie *et al*., 2012), our surface deployments should generally be a reflection of macro-jelly populations in the mixed layer. However, we cannot preclude finer-scale habitat partitioning (e.g. Briseño-Avena *et al*., 2020; Treible *et al*., 2022) within the mixed layer, particularly when seas are calm and vertical mixing is reduced, or peak distributions in the thermocline or even below it (situations that would make our values underestimates). Different factors can change the depth of the mixed layer seasonally, as well as across or along the shelf (Sarkar, 2007). During summer, the mixed layer along the Seward Line is as shallow as 10 m depth at coastal stations and 20–25 m depth at mid-shelf and basin stations (Sarkar, 2007). It is unlikely that most macro-jellyfish were confined to only the upper 3 m fished by the Methot. Assuming even distribution throughout the mixed layer our catches would only represent 10–20% of the total jellyfish present within the water column during summer and early fall. In contrast, if jellyfish avoid the surface (e.g. Jaspers *et al*., 2018), then we have underestimated biomass even more, or overestimated it if species are concentrated near-surface. Furthermore, our samples were only collected during night-time. Differences in abundance of medusae between day and night have been previously

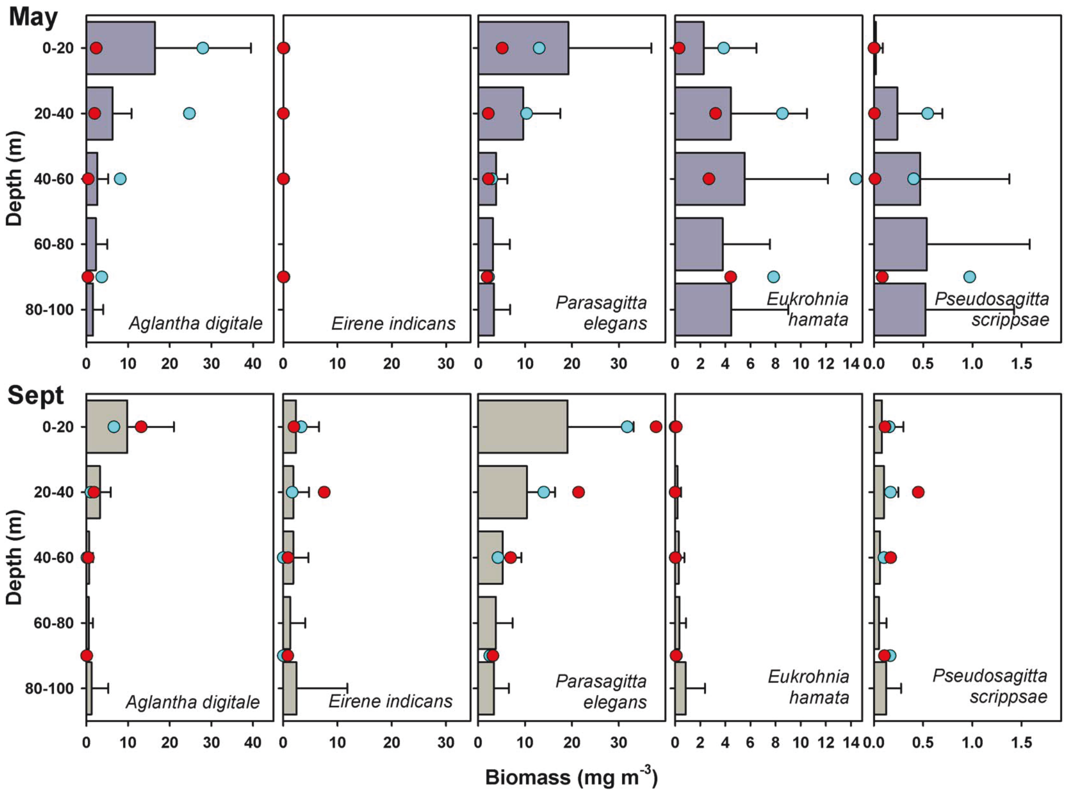

Fig. 8. Biomass of the dominant small jellyfish (*Aglantha digitale* and *Eirene indicans*) and chaetognath species (*Parasagitta elegans*, *Eukrohnia hamata* and *Pseudosagitta scrippsae*) along the Seward Line from 1998 to 2017. Bars represents averages for strata over the upper 100 m and error bars represent standard deviation over the first 21 years of sampling. Study years 2018 (blue circles) and 2019 (red circles) are plotted separately.

reported for the Bering Sea, where *C. melanaster* and *Aequorea forskalea* were concentrated primarily in the surface layer both day and night, but night-time catches were higher than during day, suggesting some degree of diel migration (Zavolokin, 2010). In contrast, the greatest concentration of *P. camtschatica* occurs in deeper layers, with no indication of substantial diurnal migrations, while *P. lactea* can undergo substantial diurnal vertical migrations (Zavolokin, 2010). Once again, these issues may be better explored in the future with *in situ* imaging approaches than net-based sampling, however at present imaging volume remains a major challenge for routine assessment of the macro-jellyfish.

Ecosystem role

Some researchers speculate that small species of jellyfish might be more numerous and more important predators upon zooplankton and ichthyoplankton than large jellyfish (Purcell and Arai, 2001; Purcell *et al*., 2010), while others contend that small hydromedusae predation on zooplankton and ichthyoplankton is of minor importance compared with that of the macro-jellyfish such as *Aurelia* (Hansson *et al*., 2005) or *Chrysaora* (Decker *et al*., 2018). Based on our observations, it appears that macro-jellyfish contain at least 10 times the biomass of other major planktonic predatory groups in the NGA, particularly within the mixed layer where most of the biomass of these predators was also concentrated (i.e. hydromedusae: *A. digitale* ~13 mg m^{-3} and *E. indicans* ~2.4 mg m^{-3}; chaetognath: *P. elegans* ~19 mg m^{-3}, averaged for May and September). However, despite several attempts to quantify the predatory effect of jellyfish, it is still unclear to what degree large jellyfish are predators upon versus competitors of fish (e.g. Olesen *et al*., 1994; Purcell, 2003; Hansson *et al*., 2005; Flynn *et al*., 2012; Decker *et al*., 2018).

Based on trawling during research surveys (Ruzicka *et al*., 2020), it has been speculated that the predatory impact of macro-jellyfish in the GoA was low compared to the Bering Sea biomass estimate (~0.12 g WW m^{-2} for *C. melanaster* for the GoA, Ruzicka pers. com.). If we instead use this study's estimate of ~1 g WW m^{-3}, and assume our nets are representative of the entire mixed layer (~25 m thick on average), then there were ~25 g

WW m^{-2} during both July and September for the macro-jellyfish combined during both 2018 and 2019. This value is 200-fold larger than the Ruzicka *et al.* estimate for GoA, and even 20 times their "high-jellyfish year" biomass estimate for the Bering Sea. Given the cyclic increases and crashes of macro-jellyfish within the Bering Sea (Decker *et al.*, 2023) and elsewhere (Condon *et al.*, 2013), is difficult to know how representative this study's two years may be without continued observations, but the data presented here suggest it is much higher than currently appreciated.

Given increased scrutiny of the status of marine species, global concern and debate is ongoing regarding jellyfish populations. In particular, it has been postulated that jellyfish biomass has been increasing over time (Brotz *et al.*, 2012; Condon *et al.*, 2012; Pitt *et al.*, 2018), which could increase predation pressure on early life stages of fish and/or competing for zooplankton prey (Gorbatenko *et al.*, 2009; Robinson *et al.*, 2014; Jaspers *et al.*, 2015; Opdal *et al.*, 2019). Although the latest trophic studies for the Bering Sea found a negative correlation between jellyfish and fish (Opdal *et al.*, 2019; Ruzicka *et al.*, 2020), these did not discount that higher-quality datasets might better elucidate the tropic role of jellyfish. Acknowledging that changes in gelatinous biomass could have profound effects on fisheries, we echo the argument that jellyfish should be more quantitatively monitored in highly productive ecosystems (e.g. Hay, 2006; Brodeur *et al.*, 2008). Long-term datasets of gelatinous zooplankton abundance, biomass and spatio-temporal distributions are relatively sparse (Mills, 2001; Robinson and Graham, 2013; Lüskow, 2020; Decker *et al.*, 2023), but essential to understand their role in the food web (Han and Uye, 2009; Purcell, 2009; Robinson *et al.*, 2014; Chiaverano *et al.*, 2018; Decker *et al.*, 2018) and how that role may be changing over time (Richardson *et al.*, 2009; Condon *et al.*, 2013; Pitt *et al.*, 2018).

CONCLUSIONS

Large jellyfish may be relatively rare numerically on continental shelves and in offshore waters of the GoA, but their WW biomass is relatively large. Their biomass is much greater than the smaller gelatinous carnivores in this ecosystem, by one to two orders of magnitude. As such, we believe they should be routine components of ecosystem assessment, despite the logistical challenges of sampling them accurately. Given the variable and cyclic fluctuations of jellyfish populations, regular and long-term observations will be required to fully assess their importance and potential impact on other ecosystem components.

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

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DATA AVAILABILITY

Data from field sampling are available under the NGA-LTER archive at DataONE.

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