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ORIGINAL ARTICLE

Seasonal hydromedusan feeding patterns in an Eastern Boundary Current show consistent predation on primary consumers

MARCOCORRALES-UGALDE[1,*], **SU SPONAUGLE**[2,3], **ROBERT K. COWEN**[3] AND **KELLY R. SUTHERLAND**[1]

[1]OREGON INSTITUTE OF MARINE BIOLOGY, UNIVERSITY OF OREGON, 473 ONYX BRIDGE 5289 UNIVERSITY OF OREGON EUGENE, OR 97403-5289, USA, [2]DEPARTMENT OF INTEGRATIVE BIOLOGY, OREGON STATE UNIVERSITY, 3029 CORDLEY HALL CORVALLIS, OR 97331, USA AND [3]HATFIELD MARINE SCIENCE CENTER, OREGON STATE UNIVERSITY, 2030 SE MARINE SCIENCE DRIVE NEWPORT, OR 97365, USA

*CORRESPONDING AUTHOR: mcugalde88@gmail.com

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Cnidarian jellyfish can be dominant players in the food webs of highly productive Eastern Boundary Currents (EBC). However, the trophic role of inconspicuous hydromedusae in EBCs has traditionally been overlooked. We collected mesozooplankton from five stations along two cross-shelf transects in the Northern California Current (NCC) during winter and summer of 2018–2019. We analyzed gut contents of 11 hydromedusan species and the prey community to (i) determine prey resource use by hydromedusae and (ii) determine temporal shifts in the trophic niche of hydromedusae, focusing on the two most collected species (*Clytia gregaria* and *Eutonina indicans*). Hydromedusae in the NCC fed mostly on copepods, appendicularians and invertebrate larvae. Nonmetric multidimensional scaling of hydromedusan diets showed seasonal shifts in prey resource driven by the abundant *C. gregaria*, which fed mostly on copepod eggs during winter and fed mostly on appendicularians and copepods during summer. Prey selectivity for copepod eggs increased during winter for *C. gregaria* and *E. indicans*. Intriguingly, theoretical ingestion rates show that both species acquire similar amounts of carbon during upwelling and nonupwelling conditions. Hydromedusae's consistent presence and predation impact across seasons may lead to significant effects in carbon and energy transfer through the NCC food web.

KEYWORDS: zooplankton; upwelling; trophic ecology; neritic; Cnidaria

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INTRODUCTION

Cnidarian jellyfish predation has been highlighted as a key process in structuring the food webs of highly productive Eastern Boundary Current (EBC) upwelling zones (Suchman *et al.*, 2008; Ruzicka *et al.*, 2012, Zeman *et al.*, 2016; Hays *et al.*, 2018). These studies have focused on large, conspicuous scyphomedusae and ignore the potential trophic role of small hydromedusae in EBCs. Hydromedusae comprise 80% of all medusan diversity (Costello *et al.*, 2008), are present in many coastal systems with seasonal upwelling (Buecher and Gibbons, 2003; Miglietta *et al.*, 2008; Rodriguez *et al.*, 2017,) and multiple species can simultaneously increase in abundance during upwelling (Hosia and Båmstedt, 2007; Miglietta *et al.*, 2008; Luo *et al.*, 2014). Such increases in hydromedusan abundance imply an enhanced predation pressure on prey populations. Highly selective feeding by hydromedusae can alter the community composition of lower trophic levels, by reducing the standing stock of planktonic invertebrates (Larson, 1987; Daan, 1989; Matsakis and Conover, 1991) and fish eggs and larvae (Purcell *et al.*, 1987; Purcell and Grover, 1990). Given the importance of EBCs for maintaining some of the world's largest fisheries, it is necessary to understand the cumulative effects of multiple hydromedusan predation pressures on EBCs plankton community structure.

Hydromedusae prey resource use can be determined by taxon-specific feeding strategies. All hydromedusae use tentacles and oral lips to capture prey, but differences in nematocyst type (Purcell and Mills, 1988) and feeding behavior (Costello and Colin, 2002) define their feeding guilds. "Sit-and-wait" Trachymedusae (i.e. *Aglantha* spp.) and Anthomedusae (i.e. *Leuckartiara* spp., *Proboscydactyla* spp.) rely on prey motion to initiate encounters, and are capable of capturing active, hard-bodied prey such as copepods and crustacean nauplii larvae (Hansson and Kiørboe, 2006; Regula *et al.*, 2009). "Current-feeding" Leptomedusae (i.e. *Clytia* spp., *Eutonina* spp. *Mitrocoma* spp.) entrain prey in the fluid vortices produced during their swimming behavior and consume mostly slow swimmers and passive prey such as other gelatinous taxa and invertebrate eggs (Purcell and Grover, 1990; Costello and Colin, 2002). However, medusan prey selection patterns and predation impact are not fixed, and temporal shifts in hydromedusan prey resource use and ingestion rates have been documented in coastal ecosystems (Hansson *et al.*, 2005; Marques *et al.*, 2015; Morais *et al.*, 2017). It is unclear if these shifts in prey resource use indicate optimal feeding periods for these medusae and to what extent their trophic impact can vary across seasons and environmental conditions.

Although feeding strategies limit the types of organisms that hydromedusae capture, prey abundance and community composition ultimately control what predators consume (Miller *et al.*, 2010). In the Northern California Current (NCC), temporal variation in climate can lead to changes in the community structure of zooplankton (Bi *et al.*, 2011; Suchman *et al.*, 2012), which result in shifts between species interactions (Francis *et al.*, 2012) and food web structure (Ruzicka *et al.*, 2012). For example, studies focusing on larval fish predation have shown that temporal shifts in planktonic prey composition can modify the trophic level and niche of larval fishes (Brodeur and Pearcy, 1992). During warm and low-productivity years of the NCC, there is high species richness and a low abundance of planktonic prey. This causes a decrease in the dietary overlap of larval fishes and an increase in their trophic position. During cold, high productivity years of the NCC, the reverse scenario occurs and a low species richness coupled with high abundance of prey in low trophic levels cause an increase in larval fish diet overlap and a decrease in their trophic position, since the fish are feeding on prey that occupy lower positions in the food web (Brodeur and Pearcy, 1992).

In contrast to vertebrate carnivores such as fish, hydromedusan effects on the NCC food web are poorly understood. Although time-series studies show a negative correlation between hydromedusa abundance and krill egg abundance in the NCC (Francis *et al.*, 2012), this correlation is limited to one hydromedusan species (*Clytia* sp.), and does not discern the biological interactions (competition, predation, etc.) that link hydromedusan abundance in the NCC to zooplankton community structure.

The goal of this study was to quantify the seasonal variation of hydromedusan trophic interactions in an EBC upwelling zone. We analyzed the gut contents of individual hydromedusae and background prey along two longitudinal transects in the NCC during summer and winter of 2018–2019. The data were used to determine whether prey consumption patterns and prey selection of co-occurring hydromedusan species shift between seasons with distinct productivity regimes and patterns of prey availability.

METHODS

Field sampling

During winter (2–14 March 2019) and summer (3–12 July 2018 and 4–27 July 2019), we collected mesozooplankton from five stations along two cross-shelf transects located in the NCC: the Newport Hydrographic (NH) line and

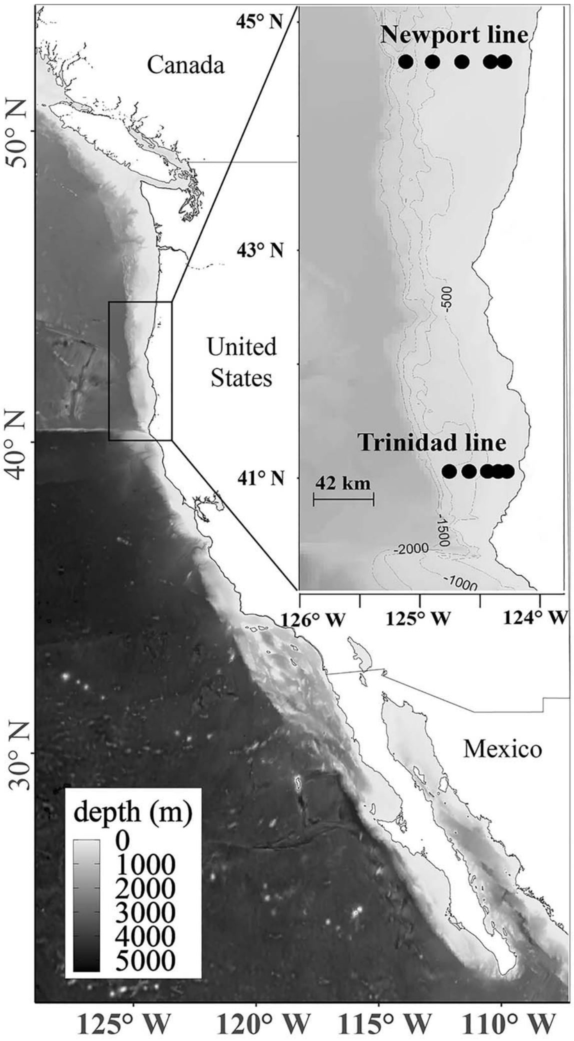

Fig. 1. Sampling stations (black points) in the Northern California Current where hydromedusae and available prey were collected during summer (3–12 July 2018 and 14–27 July 2019) and winter (2–14 March 2019). Coordinates for each station are given in Table S1.

the Trinidad Head (TR) line (Table S1). Stations along the TR transect were closer to each other due to the narrower shelf and more pronounced shelf slope in this location (Fig. 1). Mesozooplankton was sampled at fixed locations during the day with the use of a coupled multiple opening-closing net and environmental sensing system with different opening and mesh sizes (MOCNESS; MOC 1 = 1 m^2 aperture, 333 μm mesh, MOC 2 = 4 m^2 aperture, 1-mm mesh; Guigand *et al.*, 2005).

After the nets were recovered, samples were placed in a chilled petri dish for selection of hydromedusae. Hydromedusae were picked from the surface depth stratum (0–25 m) since the animals spent less time in the net (~10 min) thus decreasing the chances of gut evacuation. We obtained as many hydromedusae as possible, and we selected individuals for gut content analysis that did not have any visible damage on their swimming bells and tentacles. Selected individuals were rapidly fixed in a solution of formalin in seawater (~4% v/v). Subsequently, hydromedusa guts were inspected under a dissecting microscope. Prey were extracted from the gastrovascular cavity and from the radial canals. To quantify the background prey community, a ring-net (0.2 m^2 aperture, 100 μm mesh) was towed vertically from 0 to 25 m at the same stations where hydromedusae were collected (Fig. 1). Samples were processed in the lab following Postel *et al.* (2000). Subsamples (1–5 mL) with >200 planktonic organisms were taken with a Stempel pipette. The organisms in the subsample were enumerated and identified to the lowest possible taxonomic level.

Gut content processing and quantification

To reduce errors in the gut content data due to net feeding and gut emptying (Miller *et al.*, 2010) we quantified only the items that were found inside the gastrovascular cavity of the medusae. Prey found in the aliquot containing the preserved medusae, medusae with damaged feeding structures and prey captured but not ingested were not quantified. Net feeding does not alter hydromedusan gut content measurements, since hydromedusae retract their tentacles and do not capture prey when disturbed (Costello and Colin, 2002).

The number of prey of type i inside the guts (a_i) was corrected by prey digestion rates (Sullivan *et al.*, 1997). Species-specific digestion rates were obtained from the literature when available and extrapolated from similar prey types when unavailable (Table I). Digestion rates of invertebrate eggs by hydromedusae were obtained by feeding single *Centropages abdominalis* and *Oithona* sp. eggs to *Clytia gregaria* in the laboratory and noting the time until the ingested eggs were not visible in the gastrovascular cavity. Since digestion rates are affected by temperature (Martinussen and Bamstedt, 2001), these feeding experiments were done at constant 12°C, which is the same temperature as the water from which the hydromedusae were collected. This temperature is also within the range of the sea surface temperature reported in Oregon and California during winter and summer of 2018–2019 (Thompson *et al.*, 2019). For each prey type in the gut, the normalized number of prey (N_{ai}) was calculated as $N_{a_i} = \frac{a_i}{digestion\ time}$. The sum of all normalized number of prey (N_d) was obtained by $N_d = \sum_{i=n}^{n} N_{a_i}$. A conversion factor (CF) was then estimated by $CF = \frac{d}{N_d}$, where d was the total number of prey in the guts. The corrected number of prey of type i (a_{di}) was then obtained

Table I: Carbon weight and digestion rates used to correct prey counts in the guts

Prey type	Carbon weight (μg)	Digestion rate (hours)	Temperature (°C)	Sources
Adult copepods (*Acartia* sp.)	3	4	12–14	Larson (1987), Durbin & Durbin (1992), Suchman *et al.* (2008)
Copepod eggs	0.1	5.5	12–14	This study
Copepod nauplii	0.1	4[c]		Larson (1987)
Appendicularia (*Oikopleura* sp.)	0.5	2	12–14	King *et al.* (1980), Larson (1987)
Chaetognatha	6.64	2[a]		Canino & Grant (1985); Suchman *et al.* (2008)
Krill eggs	3.2	5.5[b]	12-14	This study
Invertebrate larvae	4[a]	4[a]	12–14	Uye (1982), Suchman *et al.* (2008)
Invertebrate larvae (barnacle nauplii)	0.5	4[c]	12–14	Larson (1987)
Veliger larvae	0.2	6	9.1	Suchman *et al.* (2008)
Others[a]	2.3 (1.5)	4.4 (1.7)	9.1	Suchman *et al.* (2008)

[a] Average of values for carbon weight and digestion time obtained for polychaetes, mollusks and gelatinous taxa from Suchman *et al.* (2008).
[b] Rate extrapolated from copepod eggs digestion rate obtained in this study.
[c] Rate extrapolated from adult copepods digestion rates.

by $a_{di} = N_{a_i} \times CF$. Subsequent analysis used a_d as the accurate estimation of ingested prey, with units of $\frac{\#prey}{individual}$ (Sullivan *et al.*, 1997; Costello and Colin, 2002).

Shifts in prey seasonal abundance and consumption patterns of the hydromedusan community

One-way Permutational Analysis of Variance (PERMANOVA) based on a Bray–Curtis similarity index was performed with environmental prey abundance data and gut content data to determine whether prey composition changed in the water column and in the hydromedusan guts in winter vs. summer. In addition, Welch's *t*-tests were performed to compare the mean prey abundances in winter vs. summer. Nonmetric multidimensional scaling (NMDS) was used to visualize seasonal shifts of prey assemblages in the environment and in the hydromedusan guts. These analyses were performed using the "vegan" package (ver. 2.5–7, Oksanen *et al.*, 2020) in the R statistical software (ver. 4.0.3). Since gut content data for *C. gregaria* and *Eutonina indicans* had a large sample size ($n = 103$ and $n = 36$, respectively) and were collected during both seasons, we focused our subsequent analysis of prey selectivity and trophic niche on these species (Fig. 2).

Determination of hydromedusan prey selectivity and ingestion rates

Gut content data for *C. gregaria* and *E. indicans* were pooled for each station and sampling date. Prey selectivity occurring in each station and season was quantified using Pearre's (1982) selectivity index, C:

$$C = \pm\sqrt{\frac{\chi^2}{n}} \tag{1}$$

where,

$$\chi^2 = \frac{n(a_d b_e - b_d a_e)^2}{abde} \tag{2}$$

with "*a*" as the prey species of interest inside the guts (a_d) and plankton (a_e), "*b*" as all other species in diet (b_d) or plankton (b_e), "*d*" and "*e*" are the total prey in diet and plankton, respectively, and "*n*" is the total number of prey in guts and zooplankton subsample. *C* is dimensionless and ranges from -1 to $+1$, with zero values representing no selection, positive values representing positive selection, and negative values representing negative selection.

Theoretical ingestion rates for individual hydromedusae (IR, $\frac{prey\ consumed}{day}$) were calculated as:

$$IR = \frac{G}{DT} \times 24$$

where G is the corrected number of prey in guts ($G = a_{di}$, see above) and DT is prey digestion time (Table I). To address whether seasons modify medusan trophic impact, we used previously published values of prey carbon content (Table I) and added all the carbon contained in each hydromedusa to calculate the individual daily carbon ingestion rate. Due to unequal sample sizes and non-normality of the data, a Kruskal–Wallis (KW) test was

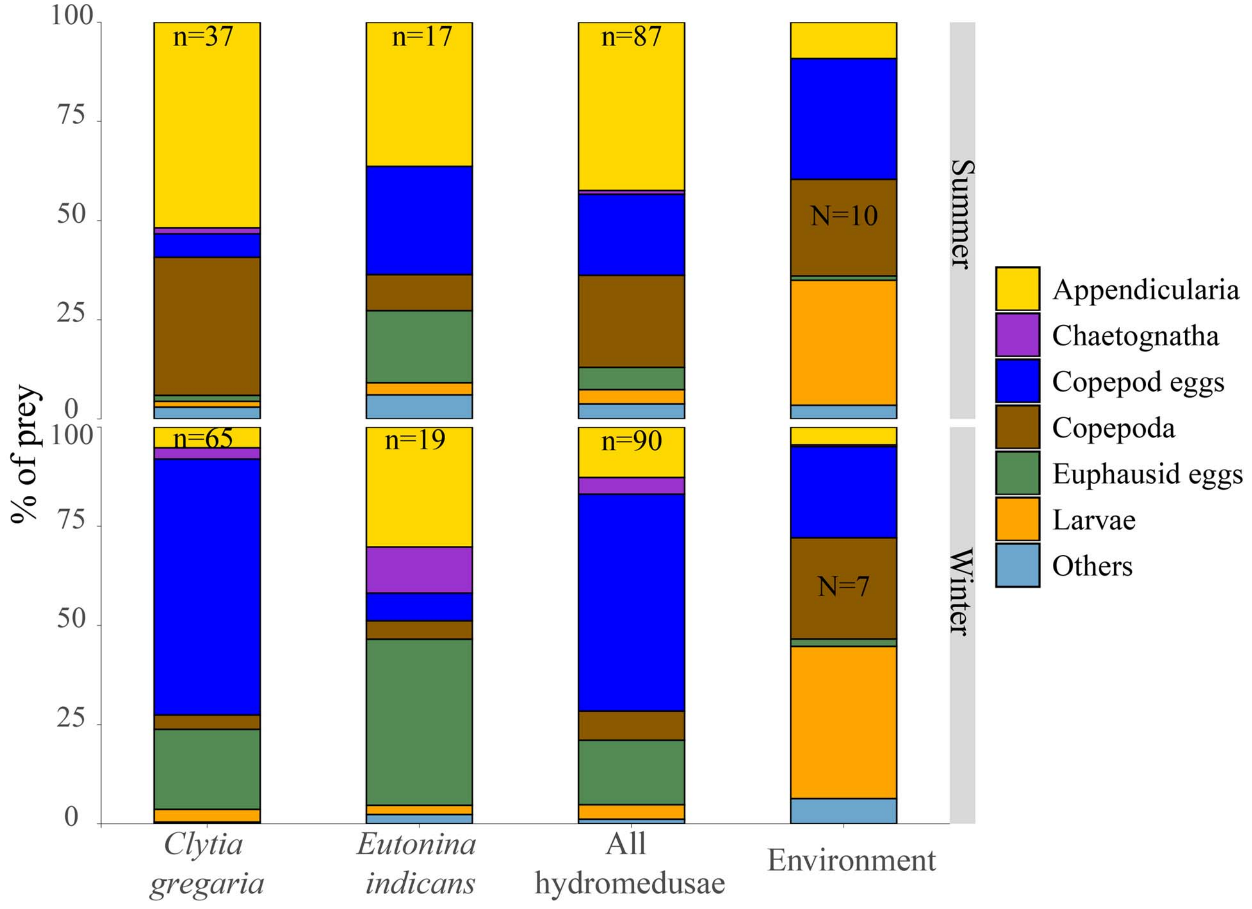

Fig. 2. Percentage of each prey type in the guts of *Clytia gregaria*, *Eutonina indicans,* all hydromedusae and prey in the environment during summers of 2018 and 2019 and winter of 2019 in the Northern California Current. N = number of ring net samples analyzed, n = number of individuals with gut contents.

used to compare the ranked average daily carbon ingestion rate for each hydromedusan species between seasons. The data distribution was analyzed with the "fitdistrplus" package (Delignette-Muller and Dutang, 2015) in R (ver. 4.0.3).

RESULTS

Hydromedusan predators and their prey in the NCC

Eleven species of hydromedusae were collected during the three cruises. From 416 medusae dissected for gut contents, 181 collected individuals had prey in their guts. Only three individuals (one *C. gregaria* and two *E. indicans*) were collected in summer 2018. A total of 632 prey items were identified (after digestion time corrections); during winter there was an average of 2.26 ± 0.16(±SE) prey in each medusan gut, and during summer there was an average of 1.90 ± 0.17 prey in each medusan gut. Nine hydromedusae (six *C. gregaria*, one *E. indicans* and two *Liriope tetraphylla*) had very digested gut contents that were not possible to identify, thus we excluded these individuals from subsequent analyses. Only *Proboscidactyla flavicirrata*, *C. gregaria*, *E. indicans* and *L. tetraphylla* were collected during both winter and summer. *Aegina citrea* was only collected during winter, and *Bougainvillia* sp., *Corymorpha* sp., *Leuckartiara* sp., *Sibogita* sp., *Mitrocoma cellularia* and *Solmissus incisa* were collected only during summer.

The hydromedusan species collected in both winter and summer consumed copepods, appendicularians and invertebrate eggs (detailed prey taxa presented in Table S2, percentage of prey ingested in Table S2). Ingested appendicularians were from the genus *Oikopleura*, copepod prey included the genera *Centropages*, *Acartia*, *Pseudocalanus* and *Oithona*. Eggs were classified according to size and presence of these items in the ring net tows as either euphausiid eggs (~500 μm diameter, Ambriz-Arreola *et al.*, 2015; Zeman *et al.*, 2018) or

Table II: Average (±standard error) corrected prey counts in Clytia gregaria and Eutonina indicans guts and prey abundances in the environment

Prey category	Summer			Winter		
	C. gregaria $N = 8$	*E. indicans* $N = 4$	Environment $N = 10$ $\left(\frac{ind.}{m^3}\right)$	*C. gregaria* $N = 7$	*E. indicans* $N = 4$	Environment $N = 7\left(\frac{ind.}{m^3}\right)$
Appendicularia	2.9 ± 0.6 (26) 11.2 ± 5.2	2.5 ± 0.7 (7) 4.1 ± 2.4	1 560 ± 344	2 ± 0.2 (18) 4.9 ± 2.6	1.2 ± 0.3 (8) 5.5 ± 2	496 ± 165
Chaetognatha	1 (1) 0.2 ± 0.2	0	6 ± 4	1.4 ± 0.2 (9) 1.2 ± 0.5	0.9 ± 0.5 (3) 1 ± 0.4	42 ± 20
Copepod eggs	2.6 ± 0.7 (9) 2.9 ± 1.5	2.3 ± 0.6 (9) 1.2 ± 1.1	5 563 ± 935	3.2 ± 0.3 (53) 19.9 ± 6.0	3.3 ± 1.0 (9) 10.6 ± 4.1	2 786 ± 798
Copepoda	1.8 ± 0.4 (22) 4.4 ± 2.4	0.8 ± 0.3 (3) 0.8 ± 0.3	4 329 ± 514	1.6 ± 0.2 (10) 1.6 ± 1	0.8 ± 0.2 (3) 0.4 ± 0.3	2 988 ± 523
Euphausid eggs	0.7 ± 0.1 (2) 0.1 ± 0.1	1.9 ± 1.4 (3) 1.3 ± 1.3	220 ± 141	2.7 ± 0.6 (19) 7.1 ± 3.0	0.9 ± 0.2 (10) 3.0 ± 1.0	179 ± 116
Larvae	1.1 ± 0.02 (2) 0.2 ± 0.1	1 (1) 0.3 ± 0.1	4 038 ± 1 277	1.6 ± 0.4 (7) 1.6 ± 0.8	0.6 ± 0.1 (2) 0.2 ± 0.2	4 532 ± 869
Others	0.9 ± 0.3 (4) 0.3 ± 0.2	1.6 ± 0.6 0.5 ± 0.3	641 ± 134	1.8 ± 0.8 (2) 0.2 ± 0.2	1.5 (1) 0.2 ± 0.2	659 ± 216

Two averages are presented for ingested prey: (i) Average prey ingested by individual medusae (no. of individuals in parentheses next to each value) and (ii) average prey ingested by station (underlined values, $N =$ no. of stations sampled, top of each column).

copepod eggs (50–180 μm diameter, Kiørboe *et al.*, 1985; Runge, 1984; Sabatini and Kiørboe, 1994). Invertebrate larvae included mostly nauplii, zoea, veligers, polychaetes and bryozoans. "Others" included hydromedusae, siphonophores, cladocerans and foraminifera. All four orders of hydromedusae found in this study consumed copepods and appendicularians. Anthoathecata and Limnomedusae also consumed invertebrate larvae. Larvae were not found in the guts of Leptomedusae and Narcomedusae.

Seasonal ambient prey availability

Prey community composition was similar in both seasons (PERMANOVA $F = 1.8228$, $P = 0.144$), but some prey abundances were higher during summer compared to winter (Table II). Significant increases in abundances during summer occurred for appendicularians and copepod eggs. Appendicularians increased from 496 ± 165 $\frac{ind.}{m^3}$ (~4.5% of total prey available) during winter, to 1560 ± 344 $\frac{ind.}{m^3}$ (~9% of total prey available) during summer (Welch's $t = 2.79$, $P = 0.016$). Copepod eggs increased from 2 786 ± 798 $\frac{ind.}{m^3}$ (~23% of total prey available) during winter, to 5 563 ± 935 $\frac{ind.}{m^3}$ (~30.4% of total prey available) during summer (Welch's $t = 2.26$, $P = 0.030$). There was an appreciable increase in copepod abundance from 2988 ± 523 $\frac{ind.}{m^3}$ (~25% of total prey available) during winter, to 4329 ± 514 $\frac{ind.}{m^3}$ (~24% of total prey available) during summer (Table II, Fig. 3) but this increase was not significant (Table S4).

Seasonal changes in prey resource use by hydromedusan predators

Although similar prey were available to hydromedusae during winter and summer, there were seasonal differences in the type of prey ingested by the hydromedusae (PERMANOVA $F = 10.337$, $P = 0.001$, Tables II and S5, Fig. 4A). More appendicularians and copepods were ingested during summer, and more copepod eggs, euphausiid eggs and chaetognaths were ingested during winter. These changes in prey resource by the hydromedusan community were likely driven by *C. gregaria*, since this species represented 57% of all the hydromedusae collected. The proportion of prey inside *C. gregaria*'s gut changed substantially between seasons. During winter, ingested prey included copepod eggs (60%), krill eggs (13%) and chaetognaths (6%) (Fig. 2a). During summer, however, most of the ingested prey were appendicularians (mostly from the genus *Oikopleura*, 46%) and adult copepods (32%, Fig. 2b) (PERMANOVA $F = 17.861$, $P = 0.001$, Fig. 4B, Table S5). Prey ingested by *E. indicans* remained similar in both seasons (PERMANOVA $F = 1.0987$, $P = 0.345$, Fig. 4C, Table S5).

Prey selectivity of sympatric hydromedusae

Prey selection patterns, indicated by Pearre's C selectivity indices, were similar between *C. gregaria* and *E. indicans* for most prey irrespective of seasons: there was positive selection for appendicularians and chaetognaths, no selection for copepods, and negative selection for invertebrate larvae (Fig. 5, Table III). However, selection for copepod

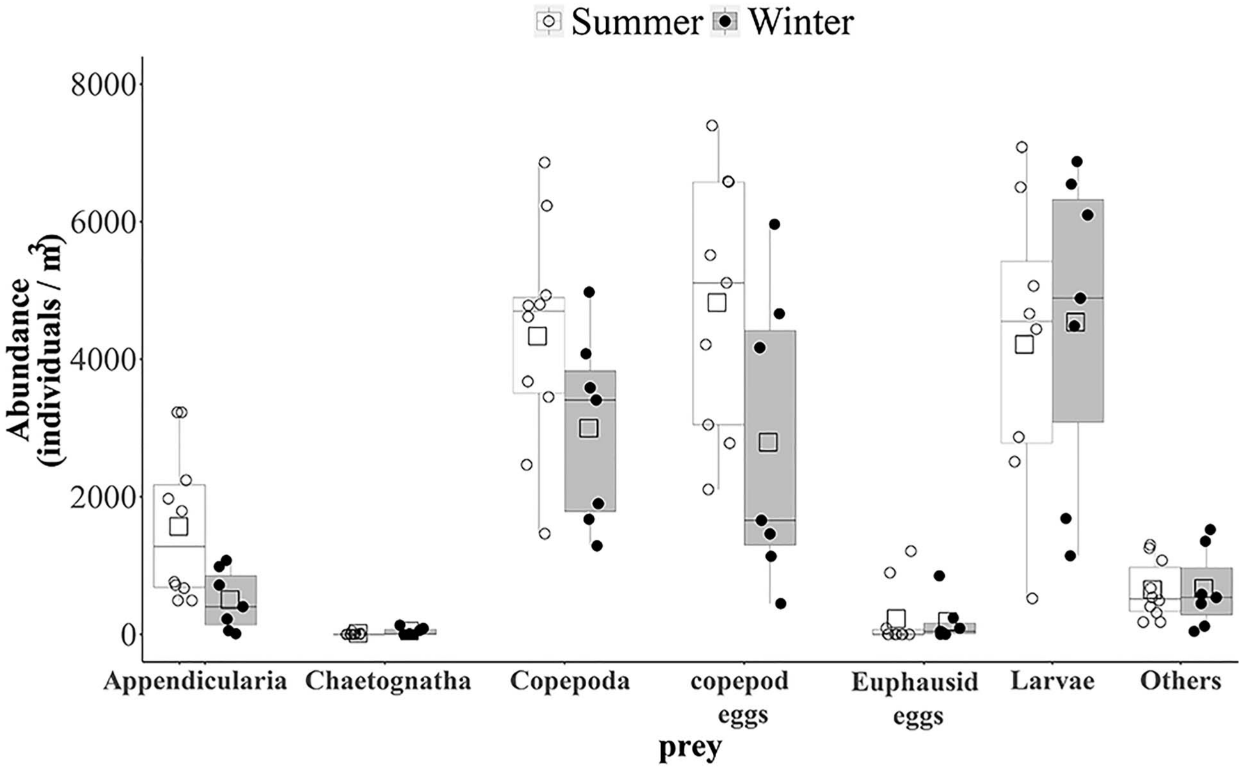

Fig. 3. Major prey groups collected with a 100 μm ring net in Northern California Current surface waters (0–25 m) during winter of 2019 and summer of 2018 and 2019. Open and solid circles represent abundances from a sample for summer and winter, respectively; open squares represent the average abundance for each prey taxa in each season. Bars represent the 25th and 75th quantiles, horizontal line inside the bar represents median, and whiskers represent 95% confidence intervals. Prey composition was similar during both seasons (PERMANOVA $F = 1.8228$, $P = 0.144$).

eggs varied seasonally and was 5–9 times greater during winter (0.25 ± 0.08 for *C. gregaria* and 0.43 ± 0.1 for *E. indicans*) than summer (-0.04 ± 0.04 for *C. gregaria* and -0.04 ± 0.07 for *E indicans*, Fig. 5, Table III).

Theoretical prey and carbon ingestion rates by hydromedusae in the NCC

Based on calculated ingestion rates, individual hydromedusae theoretically ate between 3 and 35 prey per day. For all hydromedusae, over both seasons, the highest ingestion rates were on appendicularians which were higher during summer than winter (Table IV). Despite the relative changes in prey ingestion rates by hydromedusae, carbon ingestion rates remained similar during winter and summer for both *C. gregaria* ($37.12 \pm 6.0\ \frac{\mu g\ C}{ind. \times day}$ in winter, $37.25 \pm 6.9\ \frac{\mu g\ C}{ind. \times day}$ in summer; KW $X^2 = 3.6688$, df = 1, $P = 0.554$) and *E. indicans* ($24.0 \pm 7.5\ \frac{\mu g\ C}{ind. \times day}$ in winter, $20.0 \pm 8.7\ \frac{\mu g\ C}{ind. \times day}$ in summer; KW $X^2 = 0.783$, df = 1, $P = 0.376$, Fig. 6). These carbon ingestion rates represent ~40% of the total body carbon of *C. gregaria* but only 4% of the total body carbon of *E. indicans* (body carbon data obtained from Larson, 1986 and Li *et al.* unpubl. data).

DISCUSSION

Cnidarian hydromedusae are ubiquitous members of plankton communities in EBCs such as the Humboldt Current (Rodriguez *et al.*, 2017), the Canary Current (Berraho *et al.*, 2015) and the Benguela Current (Pagés *et al.*, 1992; Buecher and Gibbons, 2003). However, very little attention has been given to hydromedusan predation in these systems. Here, we provide the first insight into predation by small hydromedusae in the NCC. The hydromedusan genera found in this study are the same as the ones found in other plankton communities (Pagés *et al.*, 1992; Miglietta *et al.*, 2008; Rodriguez *et al.* 2017), so this study provides a first approximation of hydromedusan trophic impact in coastal ecosystems with seasonal upwelling. Despite minimal differences in hydromedusan prey community composition between winter and summer in the NCC, hydromedusan prey ingestion and selection shifted between seasons, from the

Table III: Average Pearre's C prey selectivity value averaged across sampling stations (±standard error) for Clytia gregaria and Eutonina indicans

Prey type	Hydromedusae species			
	Winter		Summer	
	C. gregaria	*E. indicans*	*C. gregaria*	*E. indicans*
Appendicularians	0.30 ± 0.04 (3)	0.38 ± 0.06 (4)	0.36 ± 0.07 (8)	0.38 ± 0.19 (2)
Chaetognatha	0.07 ± 0.03 (2)	0.21 ± 0.03 (3)	0.25 (1)	–
Copepod eggs	0.25 ± 0.08 (7)	0.43 ± 0.10 (3)	−0.04 ± 0.04 (4)	−0.04 ± 0.07 (2)
Copepods	−0.09 ± 0.02 (3)	−0.09 ± 0.002 (2)	−0.003 ± 0.04 (7)	−0.005 ± 0.06 (3)
Krill eggs	0.30 ± 0.10 (4)	0.30 ± 0.07 (3)	–	0.29 (1)
Invertebrate larvae	−0.22 ± 0.06 (4)	−0.32 (1)	−0.19 ± 0.12 (2)	−0.05 (1)
Others	−0.04 (1)	0.08 (1)	0.06 ± 0.003 (3)	0.07 ± 0.02 (2)

All gut content data were corrected by digestion time for each prey type. Numbers within parentheses are sample sizes.

Table IV: Average ingestion rates (±standard error) based on published or empirically determined digestion rates of the major prey categories found in hydromedusan guts collected during winter 2019 and summer 2018 and 2019 in the Northern California Current

Prey type	Ingestion rates $\left(\frac{prey\ consumed}{day}\right)$						
	Winter			Summer			
	Clytia gregaria	*Eutonina indicans*	Others	*Clytia gregaria*	*Eutonina indicans*	*Mitrocoma cellularia*	Others
Appendicularians	24.0 ± 2.3(18)	14.8 ± 3.8(8)	12(1)	35.1 ± 6.8(26)	29.7 ± 8.1(7)	23.0 ± 5.4(6)	14.7 ± 1.6(4)
Arrow worms (Chaetognatha)	16.9 ± 3.0(9)	11.1 ± 6.4(3)	–	12.9(1)	–	16.7(1)	–
Copepod eggs	14.2 ± 1.5(53)	14.4 ± 4.3(9)	–	11.2 ± 3.2(9)	9.9 ± 2.8(9)	5.2 ± 0.9 (5)	5.0 ± 2.0(3)
Copepods	9.3 ± 1.2(10)	4.8 ± 1.2(3)	10.8 ± 4.8(5)	11.0 ± 2.3(22)	4.5 ± 1.7(3)	6.1 ± 0.9(5)	18.4 ± 8.0(4)
Krill eggs	11.8 ± 2.7(19)	3.8 ± 0.7(10)	–	3.1 ± 0.26(2)	8.4 ± 6.1(3)	4.4 ± 0(3)	9.5 ± 9.2(2)
Invertebrate larvae	9.8 ± 2.3(7)	3.4 ± 0.3(2)	6(1)	6.5 ± 0.1(2)	6.4(1)	6(1)	6.1 ± 2.3(5)
Others	10 ± 4.5(2)	8.2(1)	–	4.9 ± 1.5(4)	8.6 ± 3.1(2)	5.4 ± 0(2)	5.4(1)

Numbers in parentheses are sample size. Hydromedusan species included in "Others" are listed in Table SI.

ingestion of mostly invertebrate eggs during winter to appendicularians and copepods during summer (Fig. 4A).

This shift in prey ingestion is largely driven by the seasonal shift in prey preference by *C. gregaria* (Fig. 4B), an abundant hydromedusa in the NCC (Francis *et al.*, 2012; Briseño-Avena *et al.*, 2020), and other upwelling systems (Buecher and Gibbons, 2003; Miglietta *et al.*, 2008). This species was collected in much larger quantities ($n = 117$) than *E. indicans* ($n = 44$). *E. indicans* showed no shift in prey ingestion between seasons (Fig. 4C). However, both species had high prey selectivity for appendicularians during both seasons, and enhanced selectivity for copepod and euphausiid eggs during winter (Fig. 5). This high selectivity corresponds to the high ingestion rates obtained for these prey types (Table IV), suggesting that hydromedusae could exert a top–down control on appendicularian and copepod populations, due to the predation on adults and eggs throughout the year, and potentially compete with other planktonic predators for prey.

Hydromedusan predation impacts in the NCC

Hydromedusae might have limited effects on pelagic food webs due to their small guts and short satiation times (i.e. time to gut fullness), which results in low prey ingestion rates (Colin *et al.*, 2005; Hansson and Kiørboe, 2006). However, seasonal peak abundances of hydromedusae can be as high as those of copepods (the most abundant planktonic taxa) (Hansson *et al.*, 2005) or even higher than copepods in some portions of the NCC (Swieca *et al.*, 2020), and multiple hydromedusan species can co-occur in pelagic environments (Costello and Colin, 2002). Further, the impact of hydromedusan predation might be species-specific. In Limfjorden, Denmark, a neritic system, the dominant hydromedusae, *Sarsia* sp. and *Rathkea octopunctata*, have prey clearance rates of 0.3 $\frac{liters}{ind.\times day}$ and 0.06 $\frac{liters}{ind.\times day}$, respectively (Hansson *et al.*, 2005). The predation rates of hydromedusae in Limfjorden are lower than those of scyphomedusae and

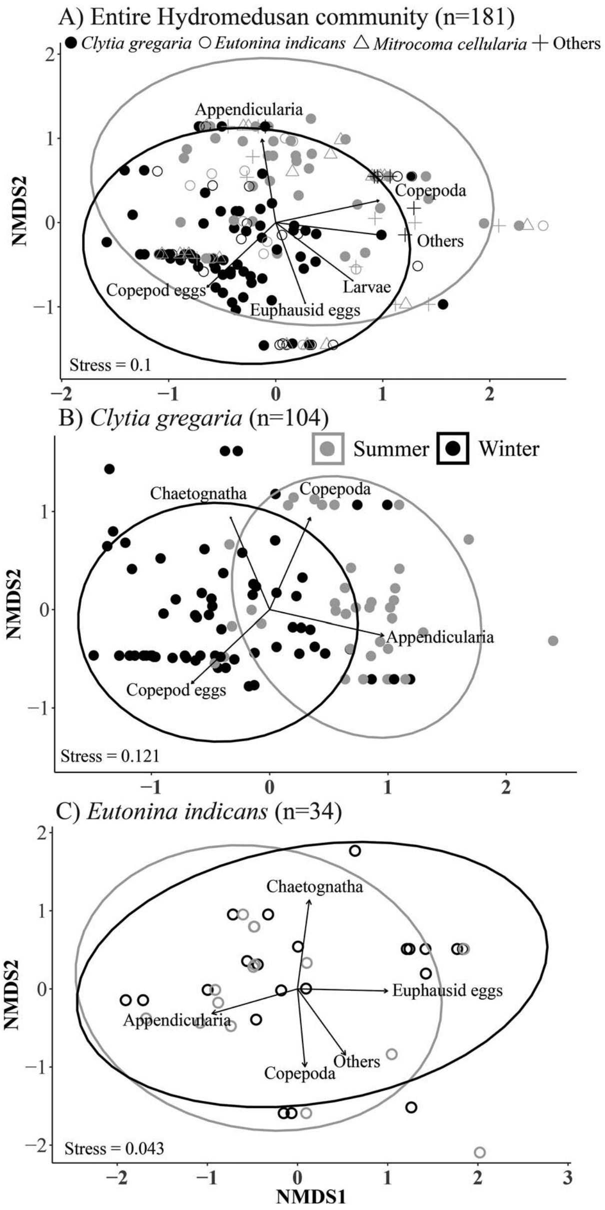

Fig. 4. Nonparametric multidimensional scaling (NMDS) plots with points representing individual medusae for (A) all hydromedusae collected, (B) *Clytia gregaria* and (C) *Eutonina indicans*. Arrows represent the direction along the axes where the prey counts for each taxon in the guts increase. Ellipses indicate 95% confidence intervals.

much lower than the theoretical maximum clearance rates for the hydromedusa *C. gregaria* ($\sim 29.8 \frac{liters}{ind.\times day}$) (Corrales-Ugalde and Sutherland, 2021). Future research could explore the cumulative impact of the entire hydromedusan community relative to other zooplankton predators in the NCC and other productive ecosystems.

If we consider *C. gregaria*'s average abundance off the central Oregon Coast ($6.7 \pm 0.5 \frac{ind.}{m^3}$, Briseño-Avena *et al.*, 2020), and the daily carbon ingestion rate presented in this study, the theoretical mass of carbon that the hydromedusan community can consume is $0.25 \frac{mg\ C}{m^3 \times day}$, which is three orders of magnitude lower than the amount of carbon an individual scyphomedusa in the NCC was estimated to consume during summer (4–41 $\frac{mg\ C}{ind. \times day}$, Suchman *et al.*, 2008). However, the year-round presence of hydromedusan predators could represent a consistent carbon flux pathway that is present when there are no large scyphomedusae. This carbon consumption rate could further be increased in patches with higher hydromedusan abundance (Swieca *et al.*, 2020).

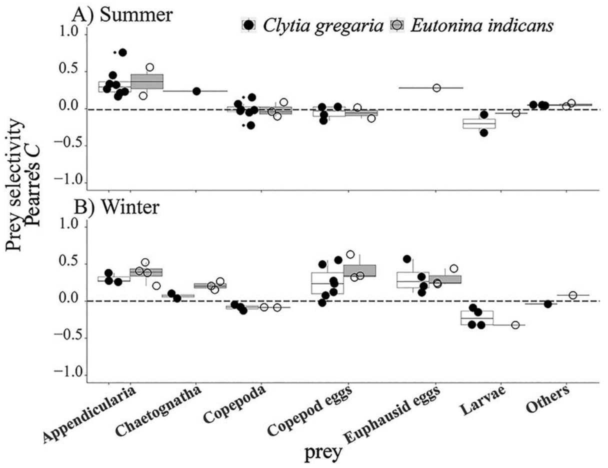

Fig. 5. Average prey selectivity (Pearre's C) values for eight major prey categories encountered in *Clytia gregaria* and *Eutonina indicans* collected in the Northern California Current for (A) summer and (B) winter. Individual data points are overlaid on box, Bars represent the 25th and 75th quantiles, horizontal line inside the bar represents median and whiskers represent 95% confidence intervals.

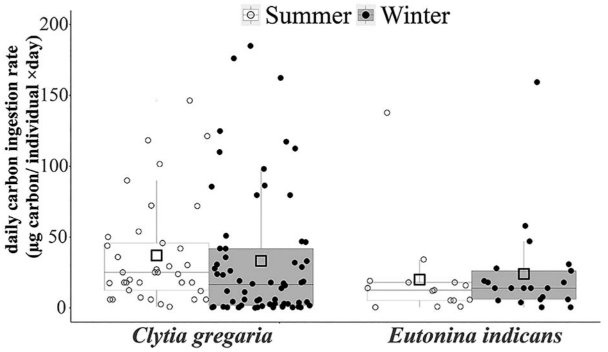

Fig. 6. Daily carbon ingestion rates for individual *Clytia gregaria* and *Eutonina indicans* in surface waters of the Northern California Current during winter of 2019 and summer of 2018 and 2019. Both *C. gregaria* and *E. indicans* consumed similar amounts of carbon during both seasons (KW $X^2 = 0.78388$, df = 1, $P = 0.376$). Individual data points are overlaid on box. Bars represent the 25th and 75th quantiles, horizontal line inside the bar represents median and whiskers represent 95% confidence intervals.

Based on the theoretical ingestion rates reported in the present study, hydromedusae could be consuming globally 0.98–3.9 $\frac{Pg\ C}{year}$, which is comparable to the 2.4 $\frac{Pg\ C}{year}$ estimated to be consumed globally by epipelagic cnidarians (Luo *et al.*, 2020). These numbers show that, first, hydromedusae might substantially contribute to the global cnidarian carbon consumption. Second, it is likely that during high hydromedusae abundance and during periods of high productivity in EBCs, hydromedusan ingestion rates are above the global average ingestion rates by other medusae.

Seasonal abundance patterns of hydromedusan prey

Hydromedusan prey abundances were similar during winter of 2019 and summer of 2018 and 2019 in the NCC (Fig. 3), which contrasts with the well documented increase in mesozooplankton abundance during summer (Peterson and Miller, 1977). Such similarities in prey abundance between seasons could be the result of the sustained presence of copepods in nearshore and shelf waters during both winter and summer. During winter, the poleward flowing Davidson Current brings warm-water neritic copepods close to shore (Hooff and Peterson, 2006). This copepod species assemblage was reported to be abundant year-round during 2018 and 2019 in the NH Line, following the positive to near neutral temperature anomalies on Oregon's continental shelf and shelf slope during this period (Thompson *et al.*, 2019). During summer, both warm-water subtropical copepods and subarctic copepod species assemblage were present nearshore (Thompson *et al.*, 2019).

Subarctic copepods are generally larger and have higher energetic value due to their lipid storage, and are associated with high energy transfer efficiency to upper trophic levels when they are consumed by predators (Hooff and Peterson, 2006). This source of high quality food is crucial for the survival of predators with high energetic demands such as larval fishes (Trudel *et al.*, 2005). However, medusozoan jellyfish have much lower energetic requirements compared to fish (Pitt *et al.*, 2013; Acuña *et al.*, 2011) and might be able to maintain optimal growth and reproductive rates with prey of variable nutritional qualities, but even they might still benefit from nutritious subpolar copepods during summer.

Trophic position of hydromedusae in the NCC

Hydromedusae in the NCC fed consistently across seasons on primary consumers (appendicularians, copepods and copepod eggs). Seasonal community transitions together with spawning periods of these organisms in the NCC results in these organisms being available for consumption throughout the year. For instance, the predominant crustacean species present during winter are planktonic grazers such as the copepods *Clausocalanus* sp., *Calanus pacificus* and the euphausiid *Euphausia pacifica* (Peterson and Miller, 1977). Both *C. pacificus* and *E. pacifica* produce eggs during winter (Brinton, 1976; Mullin, 1991) and are likely the source of the copepod and invertebrate eggs that the hydromedusae ingested during winter. During summer, several copepod species that were present in our samples (*Paracalanus parvus*, *Oithona* sp.) release or carry eggs (Peterson *et al.*, 1979). In addition, appendicularians (mainly *Oikopleura* sp.) were abundant (Fig. 3). These seasonal shifts between plankton community assemblages ensures availability of food for hydromedusae, which are able to feed on several prey types due to their diverse array of feeding strategies (Mills, 1981; Purcell and Mills, 1988; Costello and Colin, 2002; Corrales-Ugalde and Sutherland, 2021).

Given that spatial and temporal overlap of larval fishes and hydromedusae has been documented in the NCC (Swieca *et al.*, 2020), it is relevant to consider how the seasonal shifts in hydromedusan prey preference determine competitive interactions with fishes. During winter, hydromedusae could compete for prey with the English sole larvae (*Parophrys vetulus*), which feed on appendicularians (Gadomski and Boehlert, 1984), butter sole larvae (*Isopsetta isolepis*), which feed on copepodites (Gadomski and Boehlert, 1984) and sand lances (*Ammodytes hexapterus*), which feed on appendicularians and adult copepods (Hipfner and Galbraith, 2014). During summer, hydromedusae could be competing for prey with sandab larvae (*Citharichthys* spp.) and with northern anchovy (*Engraulis mordax*), both of which feed on copepodites and adult copepods (Schmitt, 1986; Rackowski and Pikitch, 1989). Going forward, studies with better spatial and temporal resolution that focus on dietary niche overlap between hydromedusae and other predators are needed to determine the nature of interspecific predatory interactions in the NCC zooplankton community.

Spatial variation of feeding interactions and prey selectivity in the NCC

Physical features such as the Columbia River Plume and upwelling fronts determine the patterns of plankton zonation in the NCC (Peterson *et al.*, 1979; Briseño-Avena *et al.*, 2020; Swieca *et al.*, 2020). For instance, certain copepod prey (i.e. *C. abdominalis*) that are ingested by Leptomedusae such as *C. gregaria* are restricted to nearshore and neritic environments (Peterson and Miller 1977, Corrales-Ugalde and Sutherland, 2021). Euphausiids also show distinct zonation in their distribution: *Thyssanoessa spinifera* is restricted to coastal environments (Smith and Adams, 1988), whereas *E. pacifica* can be abundant in offshore, more oceanic environments and these species rear eggs in different times of the year (Dorman *et al.*, 2005). However, the low spatial resolution of our station layout does not allow for inferences of how location affects hydromedusan prey selectivity, since hydromedusae were not consistently collected in all stations. The data presented here can inform future studies with *in situ* plankton camera recorders that can accurately determine the fine-scale spatial overlap between predators and prey (Swieca *et al.*, 2020).

Interannual variability in hydromedusan predation and trophic role in the NCC

Given the limitations imposed by our unequal sample sizes between summer of 2018 compared to 2019, this study was unable to address how interannual variation in NCC oceanography affects hydromedusan predation patterns. Food web modeling of the NCC has concluded that the primary production that passes through the jellyfish functional group is similar across years (Ruzicka *et al.*, 2012). A closer look at the interactions among community members of the NCC zooplankton shows strong negative effects of *Clytia* sp. on invertebrate eggs and larvae during warm periods (Francis *et al.*, 2012). Our gut content data effectively show the preference of *C. gregaria* for copepod and euphausiid eggs during 2019 (Fig. 5), during weak El Niño conditions (Thompson *et al.*, 2019). During winter and summer of 2019, the total number medusae collected (with and without gut contents) were four and three times more ($n = 209$ during winter 2019, $n = 155$ during summer 2019) than summer of 2018 ($n = 55$). This suggest that the negative interaction between invertebrate eggs/larvae and hydromedusae might be driven by an increase in hydromedusan abundance in the NCC during warm periods.

CONCLUSIONS

In the NCC, hydromedusae feed on planktonic grazers, which aligns with our current paradigm that jellyfish consume a large proportion of zooplankton grazer production in the NCC (Suchman *et al.*, 2008; Ruzicka *et al.*, 2012; Zeman *et al.*, 2016; Luo *et al.* 2020). Results of our study provide baseline data on hydromedusan diets in coastal upwelling systems, which can be extrapolated to other parts of the world's oceans with similar hydromedusan taxa (Pagés *et al.*, 1992; Miglietta *et al.*, 2008; Rodriguez *et al.*, 2017). Though hydromedusan predation may represent a smaller portion of energy transfer through the food web compared to larger scyphomedusan predators, their consistent presence and predation impact across seasons may lead to large and context-dependent interactions with their prey and other planktonic predators. Given the high diversity (Costello *et al.*, 2008) and abundances in the NCC and other coastal upwelling systems (Swieca *et al.*, 2020), further research that focuses on their spatial and temporal distributions, and dietary overlap with other predators could help us determine how hydromedusae affect the food web structure of EBCs.

SUPPLEMENTARY DATA

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

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