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RESEARCH ARTICLE

Stable isotopes reveal that gelatinous zooplankton diets group by taxonomy and feeding traits in a coastal upwelling system

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Abstract

Gelatinous zooplankton are abundant in marine ecosystems, yet their trophic roles and functional diversity in food webs have only recently gained attention. Gelatinous zooplankton taxa including hydromedusae, ctenophores, siphonophores, chaetognaths, and pelagic tunicates span multiple phyla and are often grouped taxonomically, but trait-based categorizations have emerged as an ecologically meaningful alternative. Considering their wide variety of diets and feeding modes, we examined whether gelatinous zooplankton diet diversity can be described by feeding mode or phylum categorizations. We analyzed the carbon and nitrogen stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$ values) of 490 gelatinous zooplankton samples of 32 genera/species collected across seasons and shelf positions in the northern California Current ecosystem. The $\delta^{13}C$ and $\delta^{15}N$ values fell into distinct groups when taxa were categorized three ways—by phylum, feeding mode, and feeding anatomy—indicating that both taxonomic and trait-based approaches are useful for describing the trophic diversity of gelatinous zooplankton. Even when gelatinous specimens cannot be identified taxonomically, their diets likely resemble those of taxa sharing the same feeding mode or anatomy. These insights refine our knowledge of marine food webs and facilitate the incorporation of these ubiquitous members of the food web into ecosystem models.

Gelatinous zooplankton are abundant in marine environments, and their importance as both predators and prey is increasingly recognized (Choy et al. 2017; Hays et al. 2018). Gelatinous zooplankton belong to multiple phyla and have diverse morphologies, life histories, and feeding strategies (Madin and Harbison 2001), but share the characteristics of high water and low carbon content (Lucas et al. 2011). Gelatinous zooplankton taxa include scyphomedusae, hydromedusae, siphonophores, ctenophores, pelagic tunicates, pteropods, chaetognaths, and some pelagic polychaetes (Haddock 2004) and are historically under-sampled compared to other zooplankton because of their fragile bodies. Additionally, the low carbon content of gelatinous tissues and the scarcity of identifiable gelatinous taxa in the gut contents of predators create uncertainty about the impacts of gelatinous zooplankton in marine food webs (Hays et al. 2018). Thus, in food web models, gelatinous zooplankton are often grouped into a single category or are omitted entirely (Pauly et al. 2008), though their inclusion and differentiation have been increasing (Lamb et al. 2019). Accurately incorporating these animals into food web models requires understanding their diverse roles within food webs.

In food webs, animals are often grouped taxonomically, but trait-based groupings have recently emerged as an alternative strategy for categorizing members of an ecosystem (Litchman et al. 2013; Kiørboe et al. 2018). Feeding mode governs an animal's diet and therefore may be a particularly informative trait when describing food webs (Greene 1985;

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Kiørboe 2011). Gelatinous zooplankton taxa employ a variety of feeding modes and anatomies for finding and consuming food (Purcell 1997). Active ambush feeders with a mouth remain stationary and strike prey that is detected nearby (e.g., chaetognath worms; Feigenbaum 1991), while cruise feeders with a mouth swim until they encounter prey (e.g., *Beroe* spp. ctenophores; Swanberg 1974). Passive ambush feeders with tentacles remain stationary in the water column until prey contacts their tentacles (e.g., *Aglantha digitale* hydromedusae; Costello and Colin 2002), while current feeders with tentacles entrain prey in a current they generate while swimming (e.g., *Clytia gregaria* hydromedusae; Corrales-Ugalde and Sutherland 2021). Cruise feeders with tentacles decouple the swimming current from prey encounter (e.g., *Solmissus* spp. hydromedusae; Raskoff 2002). Current feeders with lobes (e.g., *Bolinopsis* spp. ctenophores; Haddock 2007) generate a weak feeding current to draw prey toward the feeding lobes. Finally, mucous mesh feeders trap small particles on sticky meshes (Conley et al. 2018).

Among gelatinous zooplankton, feeding modes and anatomies do not necessarily correspond to taxonomic groups. For example, the phylum Mollusca includes both cruise feeders with mouths (e.g., *Clione limacina* pteropods; Conover and Lalli 1972), as well as mucous mesh feeders (e.g., *Limacina helicina* pteropods; Gilmer and Harbison 1991). Additionally, many feeding modes span multiple taxonomic groups. For example, species which feed by passive ambush with tentacles span the phyla Cnidaria (e.g., *Muggiaea atlantica* siphonophores; Purcell 1981) and Ctenophora (e.g., *Pleurobrachia bachei* ctenophores; Greene et al. 1986). The broad diversity in taxonomy and feeding traits across gelatinous zooplankton warrants further study of which categorizations are appropriate for describing gelatinous zooplankton trophic roles and for incorporating them into food web models.

Our understanding of gelatinous zooplankton diets has advanced though feeding observations and visual and molecular gut contents analysis, which provide snapshots of what individual organisms have recently consumed (e.g., Choy et al. 2017; Corrales-Ugalde et al. 2021; Damian-Serrano et al. 2022; Hiebert et al. 2025; Masterman et al. 2025). In contrast, stable isotope analysis provides information about organisms' diets across longer durations (weeks to months; Pitt et al. 2009; Schaub et al. 2021). In animal tissues, nitrogen stable isotope composition ($\delta^{15}N$ value) reflects an animal's trophic level, while carbon stable isotope composition ($\delta^{13}C$ value) can vary among sources of dietary carbon (e.g., B. Peterson and Fry 1987). Both $\delta^{13}C$ and $\delta^{15}N$ values of animal tissues are also influenced by spatiotemporal variation in the stable isotope composition of primary producers at the base of the food web (e.g., B. Peterson and Fry 1987) and taxon- and diet-specific fractionation between food source and consumer (Post 2002; D'Ambra et al. 2014; Schaub et al. 2021). Studies of gelatinous zooplankton carbon and nitrogen stable isotope composition have revealed substantial variation in trophic position among taxa (Chi et al. 2021; Hetherington et al. 2024; Chavarry et al. 2025). In the tropical east Atlantic, gelatinous zooplankton occupied more than three trophic levels (Chi et al. 2021). In the southern California Current ecosystem, gelatinous zooplankton spanned 2.4 trophic levels (Chavarry et al. 2025), and siphonophores alone spanned 1.5 trophic levels (Hetherington et al. 2024). While these studies primarily focused on variation within and among taxonomic groups, $\delta^{13}C$ and $\delta^{15}N$ values suggested connections between diet and feeding mode.

In this study, we examined the $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous zooplankton to determine whether their diets correspond to phyla, feeding modes, or feeding anatomies. We measured $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous zooplankton collected in summer and winter in the northern California Current ecosystem. This ecosystem is characterized by an eastern boundary current with wind-driven upwelling fueling high productivity on the continental shelf in summer (W. Peterson et al. 1979; Huyer 1983), allowing us to examine gelatinous zooplankton diets across seasons and productivity regimes. This work contributes to our growing understanding of trait-based structuring of ecosystems and the roles of gelatinous zooplankton within marine food webs.

Methods

Gelatinous zooplankton sample collection

In 2022 and 2023, we collected gelatinous zooplankton aboard four research cruises in the northern California Current ecosystem off the coasts of Oregon and Washington, USA. Two cruises occurred in winter during the region's "downwelling" phase (March 1–12, 2022: *R/V Sikuliaq* SKQ202204S; and February 16 to March 1, 2023: *R/V Sikuliaq* SKQ202303S), and two cruises took place in summer during the "upwelling" phase (July 18–30, 2022: *R/V Langseth* MGL2207; and August 9–21, 2023: *R/V Sally Ride* SR2317). During each of the winter 2022 and summer 2023 cruises, we collected samples at 28 stations along four 80-km latitudinal transects and two 160-km latitudinal transects spanning from the shelf to offshore regions (Fig. 1a). Due to rough weather, we sampled only 26 stations during summer 2022 and 20 stations during winter 2023. In total, there were 102 sampling events across all four cruises. This sampling scheme encompassed the extremes of temperature and nutrient supply in this region. Stations were designated as "shelf" or "offshore" by seafloor depth. Surface fluorescence decreased in stations deeper than 250 m, so this isobath was used to delineate the two regions (Fig. 1).

We collected gelatinous zooplankton samples using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) during daylight hours. The net had a 1-m^2 opening with 333-μm mesh and was towed obliquely from $\sim$ 25 m depth to the surface. At each station, a Conductivity–Temperature–Depth sensor package was also deployed to measure

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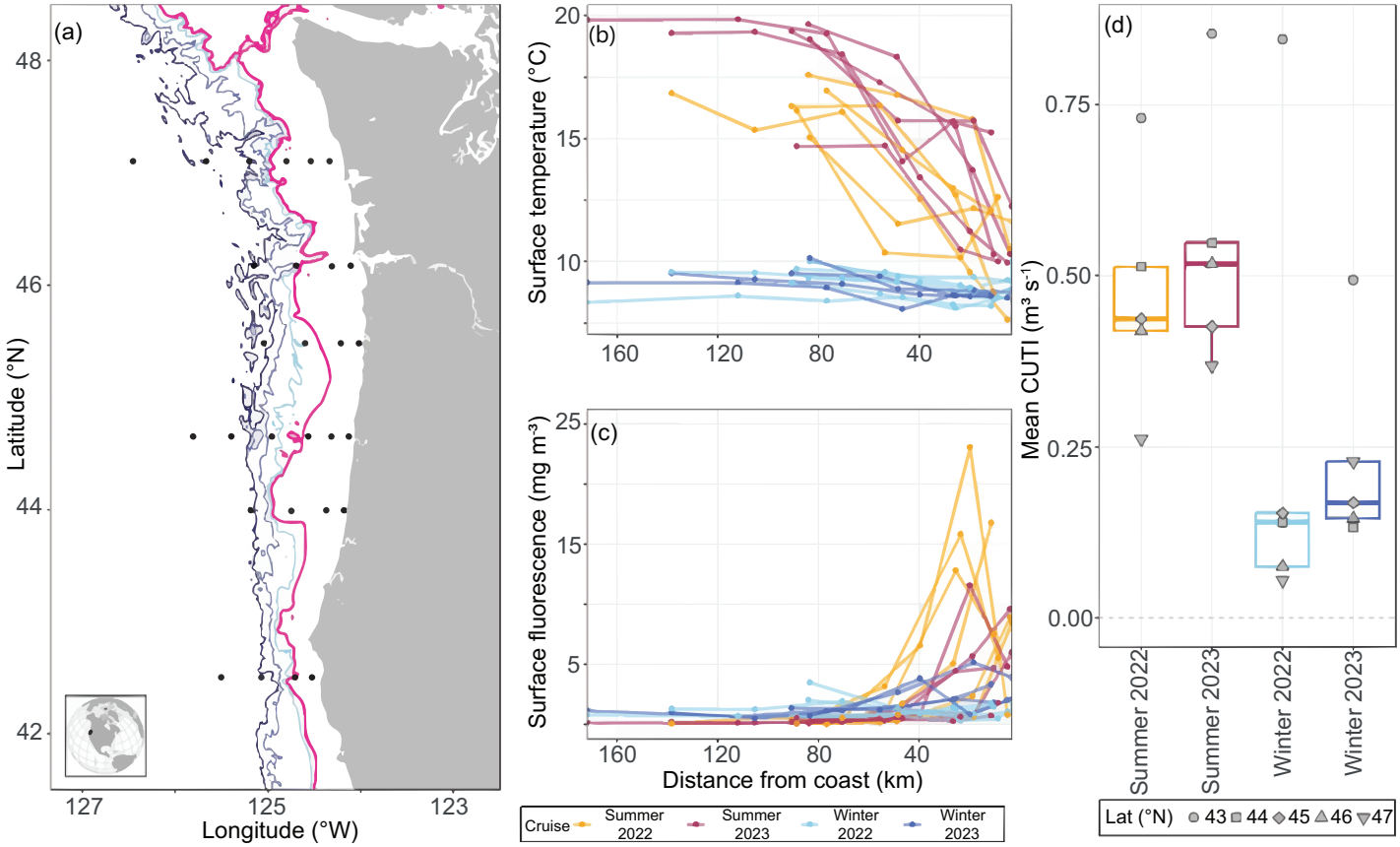

Fig. 1. Environmental conditions in the northern California Current sampling area: (**a**) Map of sampling area with sampling locations along six transects marked with points and bathymetry shown in contours. Pink contour is 250 m, delineating "shelf" vs. "offshore" regions. Blue contours light to dark are 500, 1000, and 1500 m. Bathymetry data are from GEBCO (GEBCO Compilation Group 2024). Inset shows the sampling area on a global map. (**b**) Water temperature (°C) at 5 m depth vs. distance from the coast (km). (**c**) Fluorescence (mg m^{-3}) at 5 m depth vs. distance from the coast (km). For (**b**) and (**c**), colors indicate each cruise, and lines connect measurements for each transect of each cruise. (**d**) Cumulative Upwelling Transport Index (CUTI) upwelling indices during each of the four cruises. The five points are the mean CUTI during the sampling cruise and 21 d before the cruise, with point shape indicating each degree of latitude of the sampling area (43–47°N). Boxplots summarize these mean CUTI values.

salinity, temperature, and fluorescence. Upon retrieval of the MOCNESS, we picked gelatinous zooplankton from a chilled backlit tray and grouped specimens collected at each station by the lowest identifiable taxon (genus or species-level). Samples were stored at −80°C aboard the ship and at −20°C upon return to the laboratory.

Carbon and nitrogen stable isotope analysis

In preparation for carbon and nitrogen stable isotope analysis, each gelatinous zooplankton sample was thawed at room temperature then dried at 60°C for 5 d. A few taxa had slightly different preparation methods due to organism size, the presence of shells, or colonial morphology (*see* Supporting Information Methods). Samples were then homogenized using an agate mortar and pestle. Up to 10 mg of each sample (nearest 0.001 mg) was packed in a tin capsule for analysis. Target dry sample weights were taxon-dependent, with the amount of sample chosen to produce 200–2000 μg of carbon and 20–150 μg of nitrogen per sample.

We analyzed gelatinous zooplankton samples for nitrogen and carbon stable isotope composition, reported as $\delta^{13}C$ (‰) vs. Vienna Pee-Dee Belemnite standard and $\delta^{15}N$ (‰) vs. air standard. Measurements were conducted via elemental-analyzer isotope ratio mass spectrometer at the UC Davis Stable Isotope Facility using an Elementar vario EL cube elemental analyzer coupled to an Elementar VisION IRMS (Elementar Analysensysteme GmbH) or a Sercon Europa ANCA-GSL elemental analyzer coupled to a Sercon Europa 20-20 IRMS (Sercon Ltd.). Multiple international and in-house standards were used to calibrate measurements. We corrected all $\delta^{13}C$ values for low-$\delta^{13}C$ lipid content based on their carbon-to-nitrogen ratio by mass (C : N) (Supporting Information Fig. S1) according to Post et al. (2007):

$$\delta^{13}C_{corrected} = \delta^{13}C - 3.32 + 0.99 \times C:N$$

Three gelatinous zooplankton samples were analyzed multiple times throughout the measurement runs to assess the

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precision of the gelatinous zooplankton stable isotope measurements (Supporting Information Table S1). The average standard deviation of the replicates for these three samples was 0.169‰ for $\delta^{13}C$ and 0.374‰ for $\delta^{15}N$.

Variation in stable isotope values of individual taxa (genus/species-level)

We examined the seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ values within each taxon using a Welch's two-sample *t*-test for each taxon with at least three samples collected in both summer and winter. Within each season, we also performed a t-test to compare shelf and offshore $\delta^{13}C$ and $\delta^{15}N$ values of each taxon. Additionally, we calculated the Bayesian standard ellipse area representing 40% of the $\delta^{13}C$ and $\delta^{15}N$ values of each taxon within each season using the SIBER package in R (Jackson et al. 2011). We estimated the probability (Pr) that the standard ellipse area for each taxon was smaller in summer than winter by calculating the proportion of paired posterior draws for each taxon that supported this difference.

Due to the differences in environmental conditions and $\delta^{13}C$ and $\delta^{15}N$ values between summer and winter, we separated samples by collection season for subsequent analyses. Within each season, we compared the $\delta^{13}C$ and $\delta^{15}N$ values of each taxon (with at least three samples) using global and pairwise PERMANOVA via the "vegdist" function from the vegan package (v. 2.6-10; Oksanen et al. 2025) in R followed by the "adonis2" function. We made post-hoc multivariate pairwise comparisons using the "pairwise.perm.manova" function from the RVAideMemoire package (v. 0.9-83-7; Herve 2023). Throughout this study, we applied a false discovery rate correction to the *p*-values of all tests involving multiple comparisons using the Benjamini–Hochberg procedure. We then calculated the percentage of taxon pairs within each season that had significantly different $\delta^{13}C$ and $\delta^{15}N$ values (pairwise PERMANOVA $p < 0.05$) to assess the overall distinctness of diets among taxa in summer and winter.

Variation in stable isotope values among phyla, feeding modes, and feeding anatomies

To examine whether gelatinous zooplankton diets are related to taxonomy and feeding traits, we grouped taxa by three categorizations: phylum, feeding mode, and feeding anatomy. Taxa belonged to six phyla: Annelida, Chaetognatha, Chordata, Cnidaria, Ctenophora, and Mollusca. To group taxa by feeding mode, we used seven categories based on feeding mechanisms from Kiørboe (2011) (Supporting Information Table S2). The feeding mode categories were: "mucus mesh feeding," "passive ambush with tentacles," "current feeding with tentacles," "current feeding with lobes," "cruise feeding with tentacles," "cruise feeding with mouth," and "active ambush with mouth" (Supporting Information Table S2). Because some gelatinous zooplankton taxa had similar feeding anatomy despite employing different feeding behaviors, we also grouped taxa into four feeding anatomy categories: tentacles, mouth, mucus mesh, and lobes. "Mucus mesh" and "lobes" anatomy groups were equivalent to the "mucus mesh feeding" and "current feeding with lobes" feeding modes, while "tentacles" and "mouth" anatomy groups each included taxa from multiple feeding mode groups (Supporting Information Table S2).

For each of the three categorizations, we used pairwise PERMANOVA to examine variation in $\delta^{13}C$ and $\delta^{15}N$ values among groups in summer and winter separately for all groups with at least three samples. We then calculated the percentage of pairs with significantly different $\delta^{13}C$ and $\delta^{15}N$ values ($p < 0.05$). We also calculated Bayesian standard ellipse area estimates representing 40% of the $\delta^{13}C$ and $\delta^{15}N$ values for each group within each season. We estimated the probability (Pr) that the standard ellipse area for each group was smaller in summer than winter by calculating the proportion of paired posterior draws for each group that supported this difference, as above. We then calculated the median standard ellipse area of each group and the mean of these medians across all groups to obtain a measure of "average standard ellipse area" for each categorization in each season.

Environmental data analysis

To compare summer and winter environmental conditions, we used daily Cumulative Upwelling Transport Index (CUTI) values (Jacox et al. 2018; https://mjacox.com/upwelling-indices/) for the duration of each cruise as well as 21 d prior to each cruise. We chose 21 d as the period that would influence gelatinous zooplankton stable isotope composition based on observations by Spitz et al. (2005) that zooplankton abundances responded to environmental conditions in 13–16 d. Further, the 21-d period approximated an intermediate value of stable isotope half-life estimates in scyphozoans (Schaub et al. 2021; D'Ambra et al. 2014). We conducted pairwise *t*-tests using the "pairwise.perm.t.test" function from the RVAideMemoire package to compare the upwelling strength across the four cruises using the daily CUTI values within each 1° latitude bin of the sampling area. We processed temperature and fluorescence data from the Conductivity–Temperature–Depth sensors using the oce package (v. 1.8-2; Kelley and Richards 2023). All data analysis in this study was conducted using R version 4.3.2 (R Core Team 2023) and data were visualized using ggplot2 (v.3.5.0; Wickham 2016).

Results

Oceanographic setting

Oceanographic measurements revealed distinct environmental conditions between summer and winter and between shelf and offshore regions. During summer, water temperature (measured at 5 m depth) was highest offshore (17–20°C) and lowest at the stations closest to shore (7–10°C). During winter, water temperature was low across the entire sampling region (8–10°C; Fig. 1b). Surface fluorescence (measured at 5 m depth) was lowest offshore in both seasons (0.7 mg m^{-3}). In

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summer, the mean fluorescence maximum was 10.0 mg m^{-3} and the overall maximum was 23.1 mg m^{-3}, while in winter, the mean fluorescence maximum was 2.5 mg m^{-3} and the overall maximum was 5.2 mg m^{-3} (Fig. 1c).

During all four cruises, median CUTI values exceeded zero, indicating upwelling conditions in both the summer and winter. Upwelling was about three times as strong in summer compared to winter. Daily CUTI values differed significantly between summer and winter cruises (pairwise *t*-tests, $p < 0.05$), but not between cruises of the same season in different years (Fig. 1d).

Overall carbon and nitrogen isotopic composition of gelatinous zooplankton

We measured the $\delta^{13}C$ and $\delta^{15}N$ values of 490 gelatinous zooplankton samples of 32 taxa (genus/species) from six phyla (Supporting Information Table S2) collected in summer and winter of 2 yr. Overall, samples spanned a range of 9.19‰ in $\delta^{13}C$ values and 13.44‰ in $\delta^{15}N$ values (Fig. 2). The minimum and maximum $\delta^{13}C$ and $\delta^{15}N$ values were all found offshore in winter 2023: $\delta^{13}C$ values ranged from −24.04‰ (*Clione limacina* pteropods) to −14.85‰ (*Limacina helicina* pteropods), and $\delta^{15}N$ values ranged from 2.76‰ (*Solmissus* spp. hydromedusae) to 16.20‰ (*Beroe* spp. ctenophores).

Isotopic composition of individual gelatinous zooplankton taxa (genus/species)

Within each season, there were significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values of individual gelatinous taxa identified to genus or species (PERMANOVA, $p < 0.001$). The taxa with the highest and lowest $\delta^{13}C$ and $\delta^{15}N$ values in each season are listed in Supporting Information Table S4. In summer, 19 taxa were collected, and pairwise comparisons of each taxon's $\delta^{13}C$ and $\delta^{15}N$ values to every other taxon revealed significant differences between 79% of taxon pairings (135 out of 171; pairwise PERMANOVA, $p < 0.05$). In winter, 17 taxa were

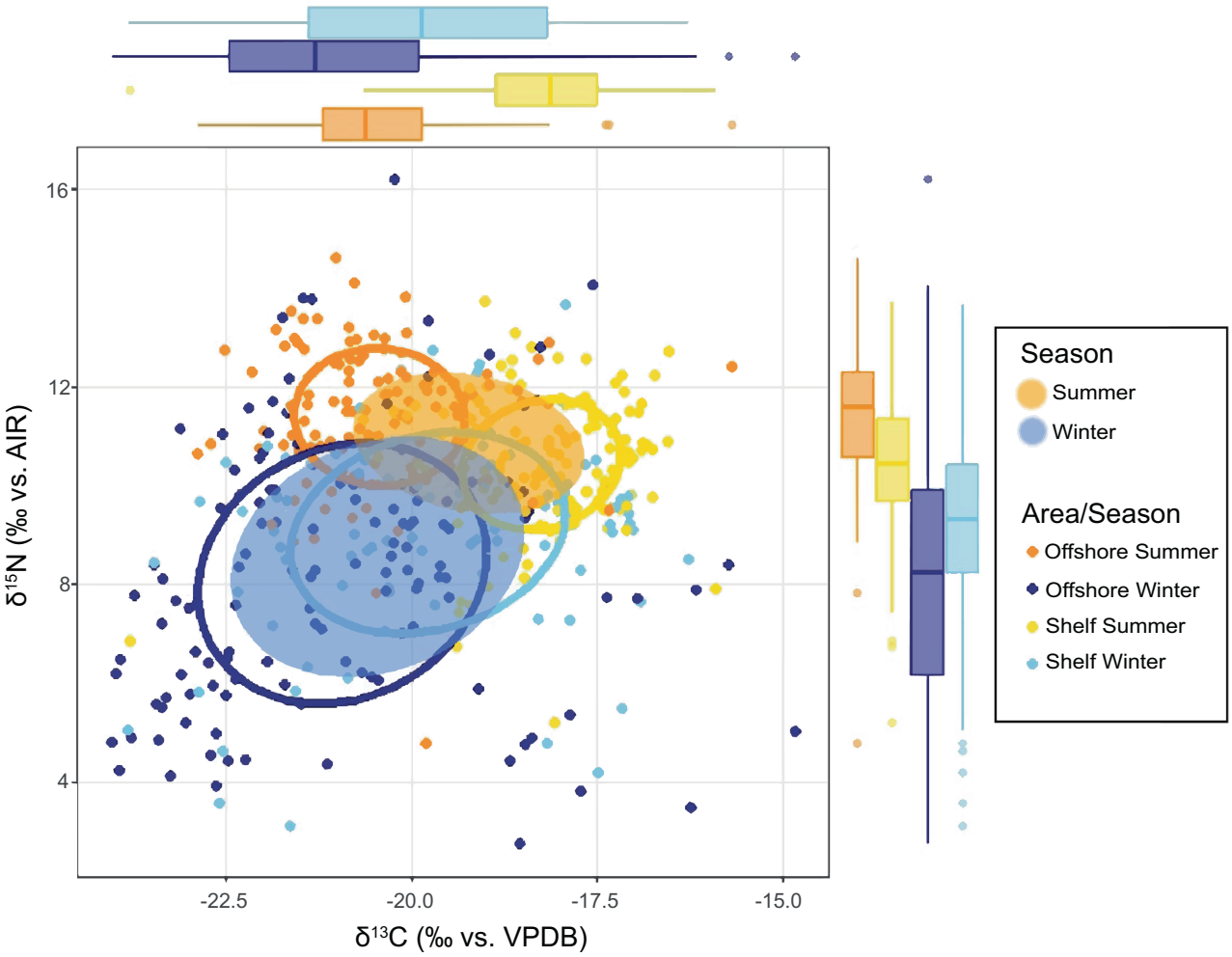

Fig. 2. $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous zooplankton taxa across seasons and shelf position in the northern California Current ecosystem. Filled ellipses are 40% ellipses for summer samples (orange) and winter samples (blue). Solid outlines are 40% ellipses for four summer/winter and shelf/offshore categories. Boxplots above and to the right of the crossplot show the $\delta^{13}C$ and $\delta^{15}N$, respectively, for each of the four seasons/areas.

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collected, and there were significant differences between 78% of taxon pairwise comparisons (106 out of 136; pairwise PERMANOVA, $p < 0.05$).

Many taxa which were collected in both summer and winter exhibited different $\delta^{13}C$ values, $\delta^{15}N$ values, and standard ellipse areas between the two seasons (Fig. 3). Five of 13 taxa collected in both seasons had significantly higher $\delta^{13}C$ values in summer, while only one taxon had a significantly lower $\delta^{13}C$ value in summer. Seven taxa had significantly higher $\delta^{15}N$ values in summer, and none had significantly lower $\delta^{15}N$ values in summer (*t*-tests, $p < 0.05$; Fig. 3; all *p*-values listed in Supporting Information Table S3). There was strong posterior support to suggest that the standard ellipse areas of five taxa were larger in winter than summer and minimal support for larger standard ellipse areas in summer (Pr > 0.95; Fig. 3c; all Pr values listed in Supporting Information Table S3). Within each season, some taxa also exhibited significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between the shelf and offshore areas. Half the taxa had higher $\delta^{13}C$ values on the shelf in the summer, but there was no consistent spatial trend in $\delta^{15}N$ values (Supporting Information Fig. S3). Since the most notable variation in $\delta^{13}C$ and $\delta^{15}N$ within taxa occurred due to seasonal differences, we separated summer and winter samples for subsequent trophic analyses.

Isotopic composition of gelatinous zooplankton phyla

When species/genera were grouped by phylum (Annelida, Chaetognatha, Chordata, Cnidaria, Ctenophora, Mollusca), all phyla were present in both seasons, but only two samples of the phylum Mollusca (one *Limacina helicina* and one *Corolla spectabilis*) were collected during the summer cruises (Fig. 4). Therefore, Mollusca was omitted from summer analyses. In summer, 9 out of 10 (90%) pairwise comparisons between phyla had significantly different isotope values when $\delta^{13}C$ and $\delta^{15}N$ values were considered together (pairwise PERMANOVA, $p < 0.05$). Cnidaria and Ctenophora did not differ significantly. In winter, 15 out of 15 (100%) phylum pairwise comparisons differed significantly in $\delta^{13}C$ and $\delta^{15}N$ values (pairwise PERMANOVA, $p < 0.05$; *see* Supporting Information Table S5 for all comparisons). We found strong posterior support to suggest that the standard ellipse areas of four out of five phyla were larger in winter than summer (Pr > 0.95), while the posterior probability of the same comparison was lower for Chaetognatha (Pr = 0.23; Pr of all phyla listed in Supporting Information Table S6). The mean of the standard ellipse areas of all phyla was 4.15‰^{2} in summer and 8.44‰^{2} in winter.

Isotopic composition of gelatinous zooplankton feeding mode groups

When species were grouped by feeding mode, all seven feeding modes ("mucus mesh feeding," "passive ambush with tentacles," "current feeding with tentacles," "current feeding with lobes," "cruise feeding with tentacles," "cruise feeding with mouth," "active ambush with mouth") were represented in summer, while "current feeding with lobes" was absent from our sample set in winter (Fig. 5).

In summer, pairwise comparison of each feeding mode to every other revealed that 20 out of 21 (95%) feeding mode pairings had significantly different $\delta^{13}C$ and $\delta^{15}N$ values (pairwise PERMANOVA, $p < 0.05$; *see* Supporting Information Table S7 for all comparisons). The exception was "current feeding with lobes" and "cruise feeding with tentacles." In winter, there were six feeding modes represented because no representatives of "cruise feeding with lobes" (*Bolinopsis* spp. ctenophores) were collected. Thirteen out of 15 (87%) feeding mode pairings had significantly different $\delta^{13}C$ and $\delta^{15}N$ values (pairwise PERMANOVA, $p < 0.05$; *see* Supporting Information Table S6 for all comparisons). The exceptions were "active ambush with mouth" and "cruise feeding with mouth" as well as "cruise feeding with tentacles" and "mucus mesh feeding." Standard ellipse areas were larger in winter than summer for "cruise feeding with mouth," "current feeding with tentacles," and "mucus mesh feeding" (Pr > 0.99; Fig. 5; Pr for all feeding modes listed in Supporting Information Table S8). The mean standard ellipse area of all feeding mode groups was 4.15‰^{2} in summer and 8.22‰^{2} in winter.

Isotopic composition of gelatinous zooplankton feeding anatomy groups

When species were categorized by feeding anatomy (tentacles, mouth, lobes, mucus mesh), all four feeding anatomies were represented in the summer, while in winter, taxa with lobes (only *Bolinopsis* spp. ctenophores in this study) were absent. $\delta^{13}C$ and $\delta^{15}N$ values of all feeding anatomies differed significantly from each other in both summer and winter (pairwise PERMANOVA, $p < 0.05$), and all feeding anatomies had larger standard ellipse areas in winter compared to summer (Pr > 0.95; Fig. 6; Pr for all anatomies listed in Supporting Information Table S9). The mean of the standard ellipse areas of all feeding anatomy groups was 4.17‰^{2} in summer and 10.55‰^{2} in winter.

Discussion

Our understanding of marine food webs is often focused on taxonomic groups, but trait-based approaches for describing ecosystems are gaining prominence (Litchman et al. 2013; Kiørboe et al. 2018). To evaluate the utility of trait-based descriptions of gelatinous zooplankton trophic roles, we explored three taxonomic and feeding-trait-based approaches to categorizing gelatinous zooplankton diets. We analyzed the carbon and nitrogen stable isotope composition of 32 gelatinous zooplankton taxa belonging to six phyla and employing seven feeding modes with four feeding anatomies. This diversity among taxa was reflected in their wide range of $\delta^{13}C$ and $\delta^{15}N$ values showing the varied roles that gelatinous taxa play in the food web of the northern California Current ecosystem. When gelatinous zooplankton taxa were categorized by

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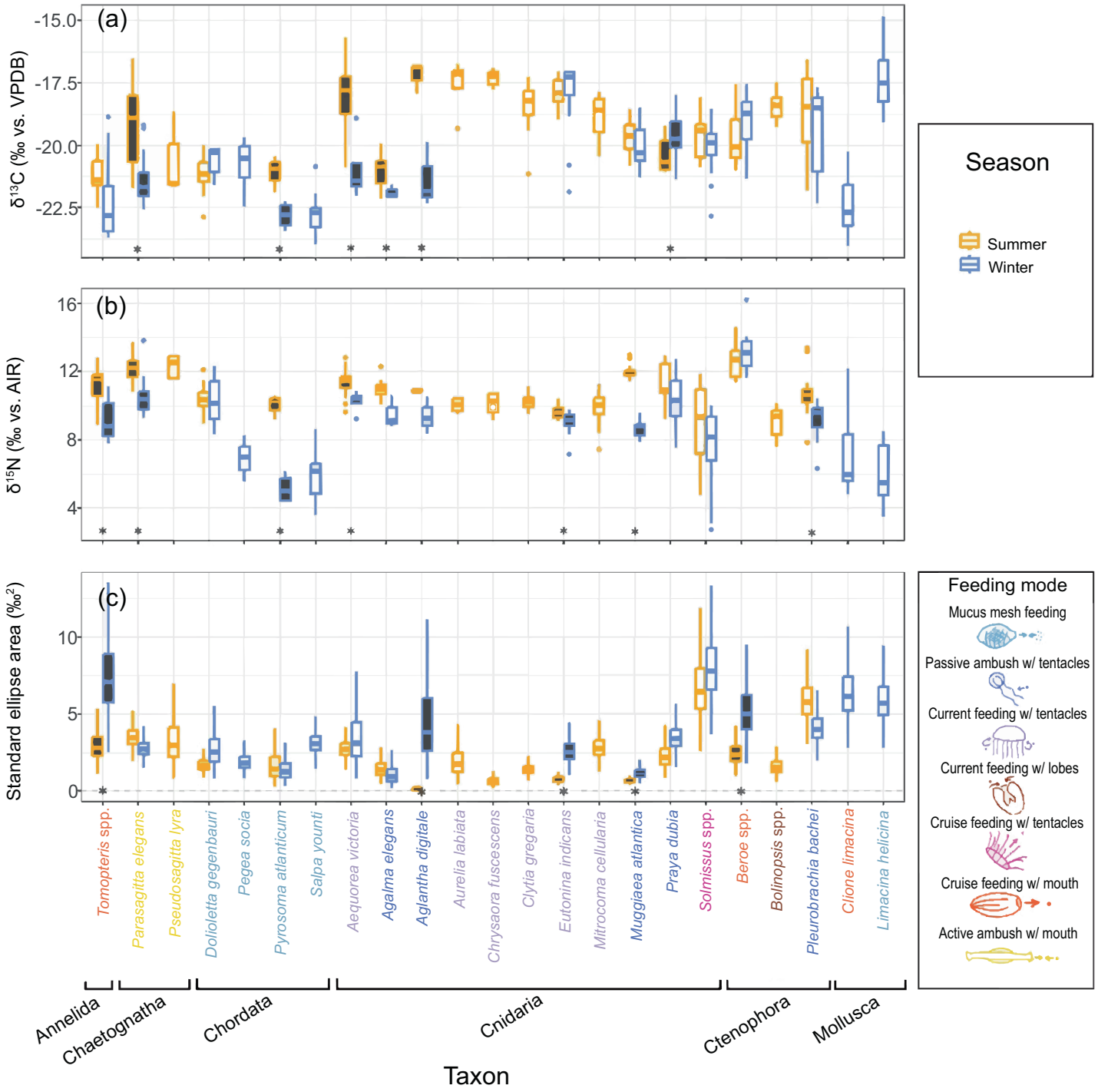

Fig. 3. Boxplots of (**a**) $\delta^{13}C$ values, (**b**) $\delta^{15}N$ values, and (**c**) Bayesian standard ellipse areas for each gelatinous zooplankton taxon in summer (orange) and winter (blue) in the northern California Current, for taxa with at least three samples in either season. In (**a**) and (**b**), $\delta^{13}C$ values and $\delta^{15}N$ values which differ significantly between summer and winter within a taxon are indicated by dark gray-filled boxes and a star on the *x*-axis (*t*-test, $p < 0.05$). In (**c**), dark gray-filled boxes and a star on the *x*-axis indicate strong posterior support for a difference in standard ellipse area between summer and winter (Pr > 0.95; all *p*-values and probabilities listed in Supporting Information Table S3). Taxon labels on the x-axis are colored by feeding mode, and phyla are indicated below the *x*-axis labels.

phylum, feeding mode, and feeding anatomy, all three categorizations resulted in a similar percentage of groups with distinct $\delta^{13}C$ and $\delta^{15}N$ values, as well as a similar average standard ellipse area in each season. These analyses suggest that, in the northern California Current ecosystem, all three taxonomic and trait-based categorizations were effective for

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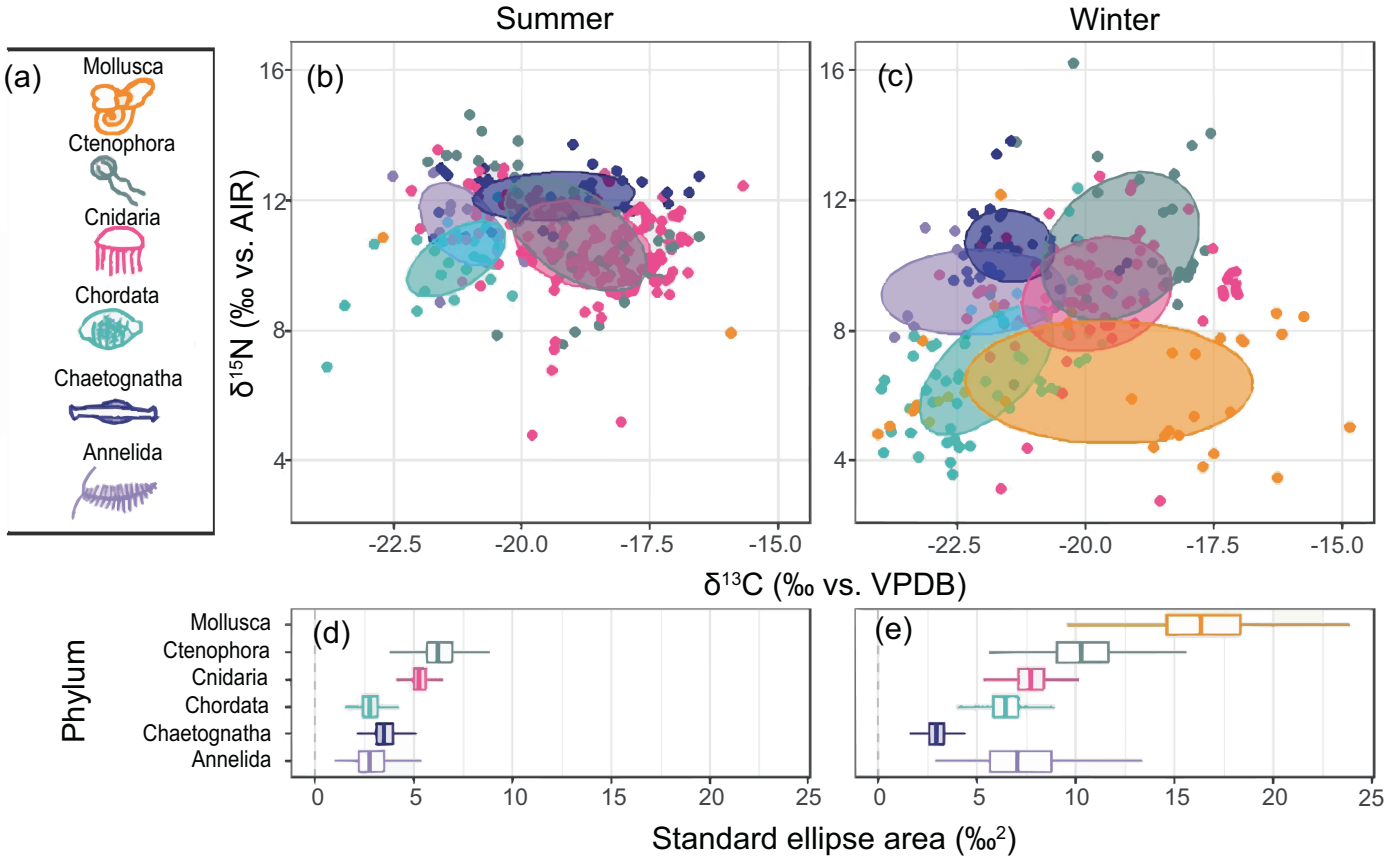

Fig. 4. Dietary resource use by gelatinous zooplankton phylum. (**a**) Diagram of representatives of six phyla included in this study, colored to correspond to (**b**–**e**). (**b**, **c**) Crossplots of the $\delta^{13}C$ and $\delta^{15}N$ values of each gelatinous zooplankton sample colored by phylum, with 40% standard ellipse areas indicated for each phylum with four or more samples in (**b**) summer and (**c**) winter. (**d**, **e**) Bayesian standard ellipse area estimates for each phylum with four or more samples in summer and winter, respectively, calculated using the SIBER package in R.

broadly describing and differentiating gelatinous zooplankton trophic diversity. In future studies, the selection of an appropriate categorization approach—or combination of approaches—will ultimately depend on the research questions being addressed.

Taxonomic categorization: Gelatinous zooplankton phyla

The gelatinous zooplankton analyzed here included taxa from six phyla which have similar watery body composition well-suited for pelagic life arising from convergent evolution (Madin and Harbison 2001). $\delta^{13}C$ and $\delta^{15}N$ values showed that, with the exception of Cnidaria and Ctenophora in summer, gelatinous zooplankton phyla had distinct diets. Cnidaria and Ctenophora had large standard ellipse areas relative to other phyla, indicating high variation in diet between samples, which contributed to the overlap in their stable isotope values.

Besides these two phyla in summer, distinct $\delta^{13}C$ and $\delta^{15}N$ values among phyla were observed despite the ecological differences within these broad taxonomic groups as well as similarities among animals across phyla. It is therefore useful to separate gelatinous zooplankton by phylum when describing their diets, even though phyla are not direct determinants of diet. In some cases, taxonomic diversity explains ecosystem function more effectively than a functional diversity approach (Otero et al. 2020). Additionally, phylum-based comparisons may be most appropriate if diet is being investigated from an evolutionary standpoint or together with other phylogeny-informed characteristics such as morphology, physiology, or reproductive mode.

Trait-based categorization: Feeding modes

We categorized gelatinous zooplankton taxa by feeding mode because an animal's feeding mode dictates its diet (Kiørboe 2011). Zooplankton feeding modes have been described conceptually, mathematically, and through direct observation (e.g., Greene 1985; Kiørboe 2011). Although $\delta^{13}C$ and $\delta^{15}N$ values do not capture all variation in diet and are influenced by spatiotemporal variability (e.g., B. Peterson and Fry 1987), stable isotope analysis confirmed quantitatively that the majority of gelatinous zooplankton diets can be differentiated along these conceptually defined lines.

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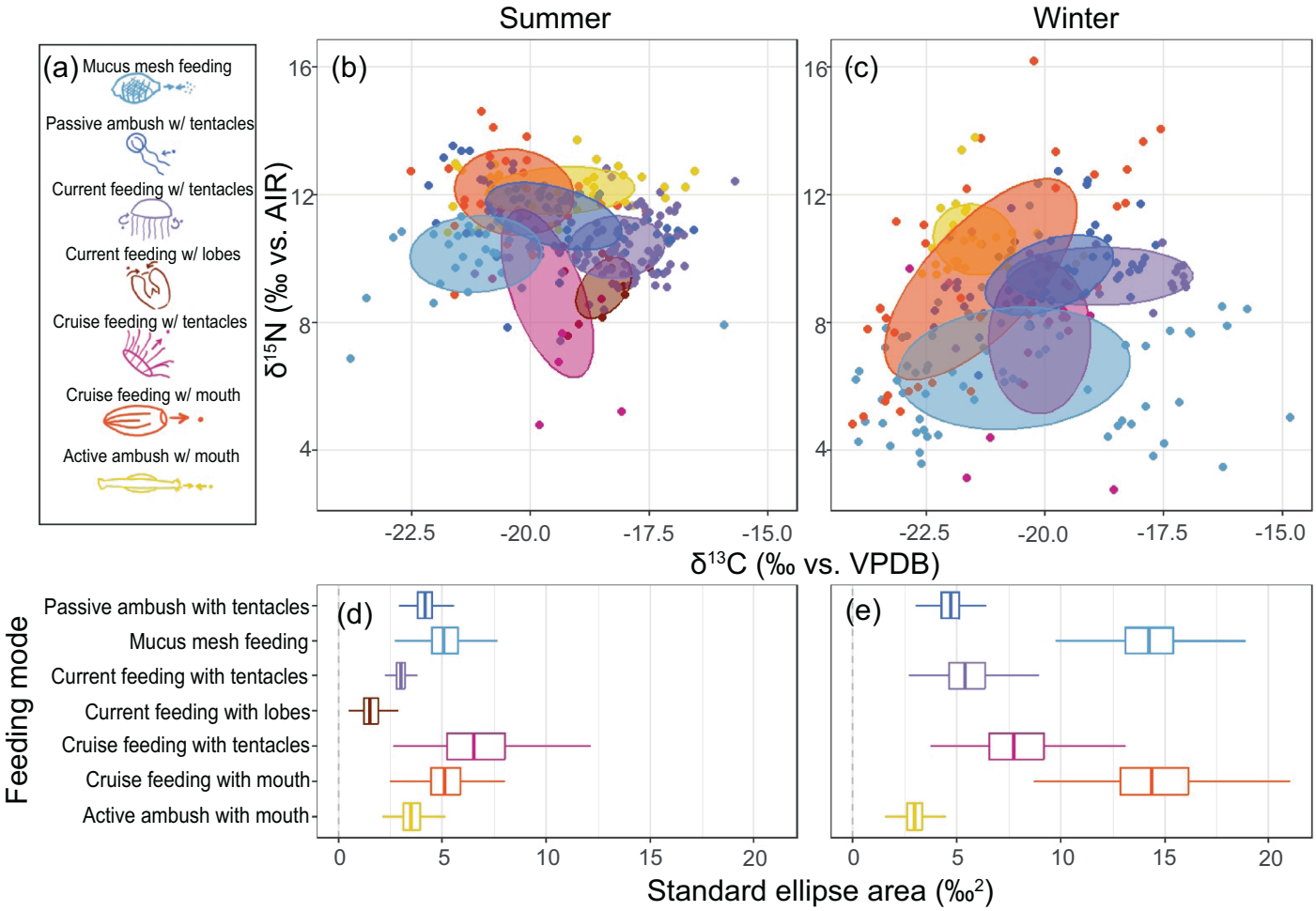

Fig. 5. Dietary resource use by gelatinous zooplankton feeding mode. (**a**) Diagram of representatives of seven feeding modes used by gelatinous zooplankton, colored to correspond to (**b**–**e**). (**b**, **c**) Crossplots of the $\delta^{13}C$ and $\delta^{15}N$ values of each gelatinous zooplankton sample colored by feeding mode, with 40% standard ellipse areas indicated for each feeding mode in (**b**) summer and (**c**) winter. (**d**, **e**) Bayesian standard ellipse area estimates for each feeding mode with four or more samples in summer and winter, respectively, calculated using the SIBER package in R.

Past studies have revealed links between feeding modes and observed diets in hydromedusae. Gut content analysis showed distinct diets between hydromedusae employing "current feeding with tentacles" and "passive ambush with tentacles" feeding modes (Costello and Colin 2002), consistent with our stable isotope data. For one hydromedusa (*Clytia gregaria*) which alternates between feeding via "passive ambush with tentacles" and "cruise feeding with tentacles," the two feeding modes have been observed to lead to distinct diets because prey that can detect and avoid the feeding current are captured only during the passive feeding (Corrales-Ugalde and Sutherland 2021). Since we could not observe actively feeding individuals in our study, we classified this species as "cruise feeding with tentacles." This highlights a strength but also a challenge of trait-based approaches such as feeding mode categories: trait-based classifications focus on individual features and interactions which can vary within taxa or populations (Kiørboe et al. 2018) and even within individuals employing discrete feeding behaviors, making them more challenging to test on a broader scale.

Unexpectedly, in summer, the two gelatinous zooplankton feeding modes which did not have significantly different $\delta^{13}C$ and $\delta^{15}N$ values were "current feeding with lobes" (in this study, only *Bolinopsis* spp. ctenophores) and "cruise feeding with tentacles" (in this study, only *Solmissus* spp. hydromedusae). These two feeding modes differ both in their feeding behavior and anatomy. Despite their differences, both feeding modes impart the ability to capture motile prey which can detect and avoid a feeding current. The feeding current generated to entrain prey during "current feeding with lobes" is undetectable by most motile prey (Cordeiro et al. 2022), and during "cruise feeding with tentacles," the tentacles are positioned outside of the fluid disturbance caused by swimming (Mills and Goy 1988; Raskoff 2002). Therefore, these feeding modes may allow for capture of similar prey types, resulting in their similar $\delta^{13}C$ and $\delta^{15}N$ values.

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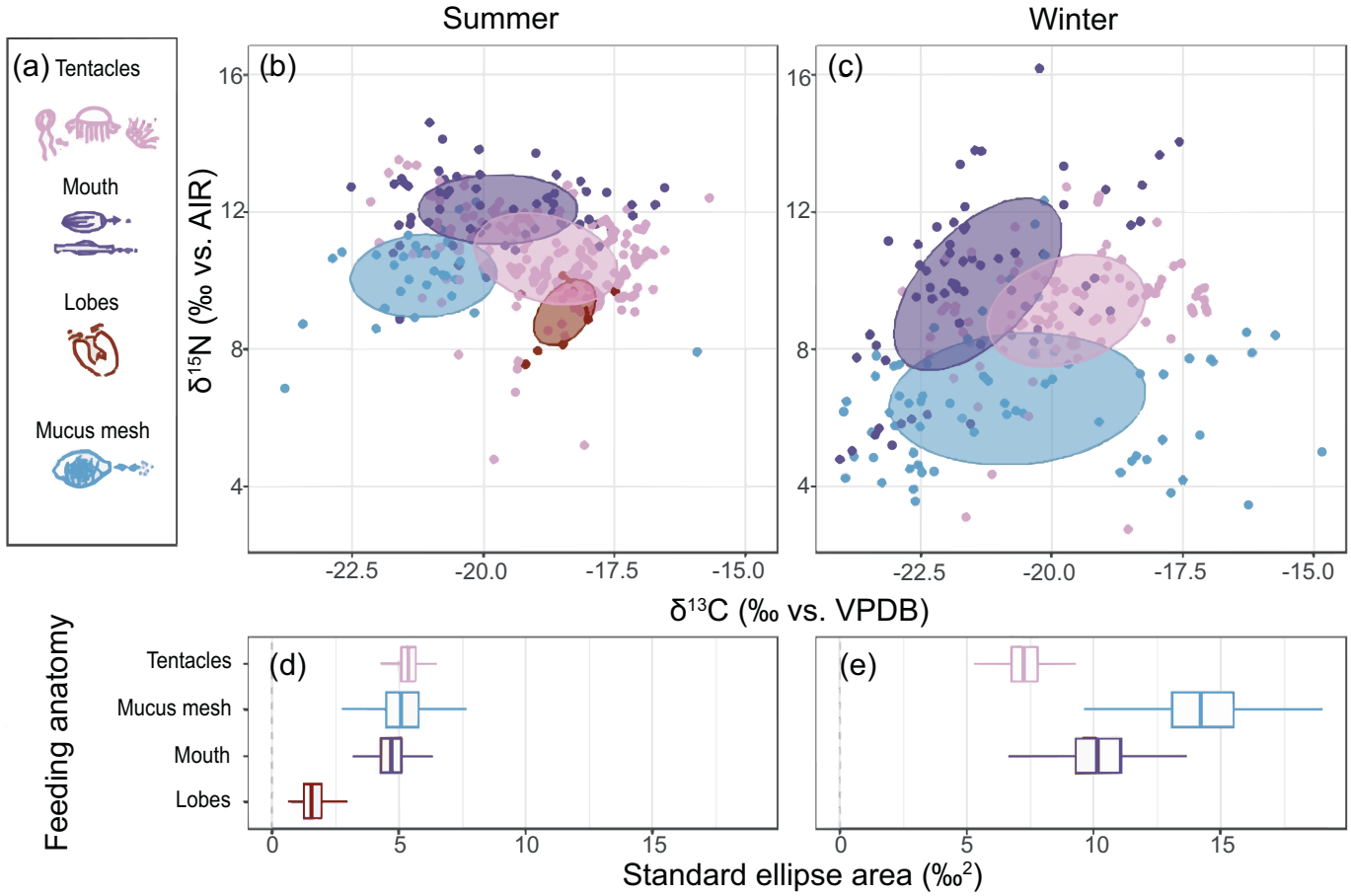

Fig. 6. Dietary resource use by gelatinous zooplankton feeding anatomy. (**a**) Diagram of representatives of four feeding anatomies of gelatinous zooplankton, colored to correspond to (**b**–**e**). (**b**, **c**) Crossplots of the $\delta^{13}C$ and $\delta^{15}N$ values of each gelatinous zooplankton sample colored by anatomy, with 40% standard ellipse areas indicated for each anatomy in (**b**) summer and (**c**) winter. (**d**, **e**) Bayesian standard ellipse area estimates for each feeding anatomy with four or more samples in summer and winter, respectively, calculated using the SIBER package in R.

"Cruise feeding with tentacles" was the feeding mode group with the highest overlap with other groups across both seasons. This likely resulted from high variation in $\delta^{13}C$ and $\delta^{15}N$ values in this group, indicated by its relatively large standard ellipse area. High variation in $\delta^{13}C$ and $\delta^{15}N$ values of "cruise feeding with tentacles" was consistent with the high prey diversity of *Solmissus* spp. and other narcomedusae observed via video in the central California Current ecosystem (Choy et al. 2017). However, the low $\delta^{15}N$ values of "cruise feeding with tentacles," on par with "mucus mesh feeding," suggest that this mode of feeding may allow for capture and ingestion of small particles unaccounted for by past studies.

Trait-based categorization: Gelatinous zooplankton feeding anatomy

Feeding modes, examined above, comprise the behavior that an animal uses to find and catch food as well as the anatomy that it uses to capture the food. Among the diverse gelatinous zooplankton, both traits vary widely and potentially interact, so we examined whether grouping by feeding anatomy alone would be informative. We found that $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous zooplankton differed when grouped by only this single trait, suggesting that feeding anatomy may be a key trait in determining diet even though it is just one component of an animal's food acquisition process.

Across both seasons, taxa feeding with a mucus mesh had relatively low $\delta^{15}N$ values and taxa feeding with a mouth had relatively high $\delta^{15}N$ values. The low $\delta^{15}N$ of taxa with a mucus mesh indicates that even large-body-size mucus mesh feeders have a low trophic level diet, directly connecting primary producers to larger predators (Sutherland and Thompson 2021). In contrast, the high $\delta^{15}N$ values of taxa with a mouth show that this feeding anatomy, which requires the predator to contact its prey without the aid of a feeding current or long appendages, generally allows for feeding at higher trophic levels than other feeding anatomies. Accounting for differences in the anatomies that gelatinous zooplankton use to acquire food can capture meaningful differences in their trophic roles.

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Inferring diets from $\delta^{13}C$ and $\delta^{15}N$ values

In this study, each sample comprised multiple individuals of the same taxon collected at the same time and location. Thus, the $\delta^{13}C$ and $\delta^{15}N$ values reflect the average diet of a taxon at a certain time and place, temporally integrated over weeks or months (Pitt et al. 2009; Schaub et al. 2021). Similar diets do not necessarily imply dietary specialization; organisms eating the same generalist diet may also have similar $\delta^{13}C$ and $\delta^{15}N$ values. Diet is determined by food selectivity, related to an animal's feeding mode (the "dietary restrictions"), but also the available food (the "menu"). Therefore, $\delta^{13}C$ and $\delta^{15}N$ values reflect the realized diets of animals within their specific ecosystem, which can vary in space and time.

Interestingly, the standard ellipse areas of many groups were larger in winter than summer across all categorizations (phylum, feeding mode, and feeding anatomy) and even within individual genera/species. This seasonal pattern occurred despite greater homogeneity in environmental conditions and similar shelf/offshore $\delta^{13}C$ and $\delta^{15}N$ values in gelatinous zooplankton in winter. Larger standard ellipse areas in winter could occur due to spatial differences in diets within taxa caused by patchy prey distributions. In the northern California Current, zooplankton cooccurrence quantified via in situ imaging showed a positive correlation with temperature indicating greater patchiness in winter (Schmid et al. 2023).

While $\delta^{13}C$ and $\delta^{15}N$ values of animal tissues reflect the diet of the animal, they are also influenced by the stable isotope composition of primary producers which can vary in space and time (e.g., B. Peterson and Fry 1987). When analyzing dietary categories of gelatinous zooplankton in the northern California Current ecosystem, we separated specimens collected in summer and winter due to the seasonally distinct environmental conditions and $\delta^{13}C$ and $\delta^{15}N$ values within many taxa.

Higher $\delta^{13}C$ and $\delta^{15}N$ values in summer across many gelatinous zooplankton taxa were likely caused by seasonal shifts in the baseline isotopic composition of primary producers rather than by shifts in gelatinous zooplankton diets. We expected higher baseline $\delta^{13}C$ values in summer due to a seasonal increase in phytoplankton growth leading to greater uptake of 13-carbon from the dissolved inorganic carbon pool (McMahon et al. 2013). No previous studies have reported winter $\delta^{13}C$ values from the northern California Current. However, studies examining the cross-shelf productivity gradient in the California Current and seasonal studies in other eastern boundary current upwelling zones have demonstrated a correlation between productivity and $\delta^{13}C$ values, suggesting that higher productivity in summer fueled by coastal upwelling may lead to increased $\delta^{13}C$ values (Miller et al. 2008; Gorbatenko et al. 2014; Castro et al. 2020; Chavarry et al. 2025).

In contrast to $\delta^{13}C$, we expected baseline $\delta^{15}N$ values to be lower in summer than winter based on the seasonal productivity patterns in the northern California Current ecosystem. More unassimilated nitrate was present in the surface water in the summer (Forgrave et al. 2025), indicating the potential for preferential uptake of nitrogen-14 by phytoplankton (Montoya and McCarthy 1995). Additionally, an increase in gelatinous zooplankton $\delta^{15}N$ values corresponding with decreasing upwelling strength, depletion of the surface nitrate pool, and increasing assimilation of nitrogen-15 by primary producers has been observed across the spring-to-fall transition in the southern California Current ecosystem (Chavarry et al. 2025). However, since we observed higher $\delta^{15}N$ values in summer compared to winter, we suspect that the isotopic composition of source nitrate shifts between winter and summer in the northern California Current, overwhelming any decrease in $\delta^{15}N$ values resulting from the selective uptake of nitrogen-14. Higher baseline $\delta^{15}N$ values in summer have been observed in the central California Current region and are attributable to nitrate from suboxic, deep-water fueling productivity during upwelling (Altabet et al. 1999). Such a change in the isotopic composition of source nitrate, rather than dietary changes, probably caused the observed increase in gelatinous zooplankton $\delta^{15}N$ values between winter and summer. Given the dynamic and episodic nature of upwelling and advection in the northern California Current region (Huyer 1983), further study on baseline $\delta^{13}C$ and $\delta^{15}N$ values throughout the year would be valuable.

In our dataset, we cannot definitively determine whether differences in $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous zooplankton within each season are due to distinct diets or spatial variation in isotopic baselines. However, we observed no systematic differences in $\delta^{13}C$ or $\delta^{15}N$ values of particulate organic matter collected on the shelf and offshore in summer 2023 (Supporting Information Fig. S2), so the influence of spatial variation in isotopic baselines on $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous zooplankton within seasons may be minimal. Even if spatial differences play a role, this is still indicative of nonoverlapping feeding habits between groups within the ecosystem.

Overall, the large range of $\delta^{13}C$ and $\delta^{15}N$ values occupied by gelatinous zooplankton reflects their diverse trophic roles in marine food webs. The overall $\delta^{13}C$ and $\delta^{15}N$ ranges observed here are within $\sim 1‰$ of the ranges of gelatinous zooplankton in the tropical east Atlantic (Chi et al. 2021) and in the southern California Current (Chavarry et al. 2025). The range of $\delta^{15}N$ values we observed in summer between gelatinous zooplankton taxa with the lowest and highest values (*Solmissus* spp. hydromedusae to *Beroe* spp. ctenophores) was similar to the range among all nekton, including juvenile forage fishes and apex predator sharks, previously recorded in this region (Miller et al. 2010). This study highlights how the vast diet diversity within gelatinous zooplankton can be described by either taxonomy or feeding traits. Even when an organism's exact taxonomy cannot be determined, its diet is likely similar to that of taxa with the same feeding mode or

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anatomy. Further exploration will inform which traits best describe gelatinous zooplankton trophic roles under varied environmental conditions, ultimately determining the most appropriate categorization for a given application or research question.

Author Contributions

Elizabeth Wallace: conceptualization, methodology, investigation, formal analysis, visualization, writing (original draft), writing (review and editing). Luke A. Bobay: investigation, writing (review and editing). Lucas C. R Silva: funding acquisition, writing (review and editing). Su Sponaugle: conceptualization, funding acquisition, writing (review and editing). Robert K. Cowen: conceptualization, funding acquisition, investigation, writing (review and editing). Kelly R. Sutherland: conceptualization, funding acquisition, investigation, supervision, project administration, writing (review and editing).

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Conflicts of Interest

None declared.

Data Availability Statement

Data from this study are available through the Biological and Chemical Oceanography Data Management Office (BCO-DMO), under the title "Carbon and Nitrogen Stable Isotope Measurements of Gelatinous Zooplankton and Larval Fish in the Northern California Current" as part of the project "Collaborative Research: Plankton size spectra and trophic links in a dynamic ocean" (https://www.bco-dmo.org/project/855248).

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