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CURRENT EVIDENCE

Integrating siphonophores into marine food-web ecology

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Scientific Significance Statement

Recent work challenges the paradigm that gelatinous animals are trophic dead ends and demonstrates their central roles as predators and prey in marine food webs. However, that research is primarily focused on scyphozoan "true jellies." We review the ecological niches of siphonophores, gelatinous cnidarians that are understudied but abundant across the water column. We discuss methodological advances that facilitate studying the diets of gelatinous animals and consider avenues for future research. Our results illustrate that siphonophores occupy numerous trophic niches. There are diet differences between siphonophore suborders and species, and our results suggest that specialization may be more predominant within deep, compared to shallow habitats. Synthesizing siphonophore predator–prey interactions highlights the diverse energy flow pathways through gelatinous components of marine food webs.

Abstract

Siphonophores are a clade of understudied colonial hydrozoans (Cnidaria) that are abundant predators in oceanic ecosystems, with species present across the water column. We (1) synthesize current knowledge about siphonophore trophic ecology and predator–prey interactions, (2) analyze siphonophore-prey networks to compare food-web topology between shallow and deep-pelagic habitats, (3) discuss contemporary techniques that will allow for more integrative studies of siphonophore feeding ecology, and (4) and present a vision for future research. We found distinct diet differences between siphonophore species, indicating that siphonophores occupy multiple trophic niches and prey on a diversity of taxa. Our results suggest that siphonophore-prey networks may be more specialized in the deep pelagic than in the epipelagic, suggesting potential trophic differences between depth habitats. This study highlights niche differentiation and trophic complexity among siphonophores and demonstrates the importance of gelatinous zooplankton in shaping food web structure in pelagic ecosystems.

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Data Availability Statement: Data that were gathered from the literature to create predator–prey networks are in the Supplementary Material. All raw data and code used for our analyses and figures are in a Bitbucket data repository titled "Siphonophore Trophic Review" created by E.D. Hetherington. This repository is publicly available: https://bitbucket.org/Ehetherington86/siphonophore-trophic-review. Additionally, we have included one .pdf file of data used for our analyses (PurcellChoy_siphdiets.PDF). The remainder of the data used in our synthesis is in the Supplementary Materials section.

Additional Supporting Information may be found in the online version of this article.

The fundamental attributes of food web structure are species richness, trophic linkages (i.e., feeding interactions), and complexity within a system (Dunne et al. 2002; Link 2002). Characterizing these attributes provides a foundation to model ecosystem structure and energy flow through food webs. However, identifying species interactions can be challenging, particularly in less accessible ecosystems like the deep-pelagic ocean (> 200 m or sub-euphotic depths) where sampling capabilities are limited, and quantifying food web relationships is challenging (Robison 2004; Libralato et al. 2014). Further, certain food web components are delicate and easily destroyed by common sampling approaches like trawling, which hinders our ability to trace food web interactions through these trophic pathways.

Gelatinous zooplankton (GZ) are soft-bodied animals that span several phyla and vary in morphology and trophic ecology. GZ were traditionally overlooked in ecological studies, as they were presumed to be non-nutritious prey for predators (Arai 2005), and "trophic dead ends" that are not consumed by many higher trophic level species. This paradigm is shifting as recent studies using contemporary sampling and analytical approaches illustrate that GZ serve key ecological roles as predators, prey, particle flux mediators, and sequestrators of carbon (Henschke et al. 2016; Choy et al. 2017; Hays et al. 2018; Chi et al. 2021). The trophic links between GZ, known as the "jelly web" (Robison 2004), are complex, as GZ feed on a wide diversity of prey and employ diverse feeding strategies (e.g., active hunters, passive trappers, filter feeders). Characterizing the specific links has been challenging, due to the difficulties associated with their collection. Moreover, most studies on GZ have put relatively more focus on scyphozoan medusae (Cnidaria: Scyphozoa) or "true jellies," with less representation from other abundant GZ that are more fragile and difficult to collect.

Siphonophores (Cnidaria: Hydrozoa) are polymorphic colonial hydrozoans with 192 described species across three historically recognized suborders: Calycophorae, Physonectae (which is paraphyletic and includes Calycophorae), and Cystonectae (Fig. 1) (Mapstone 2014). Unlike many scyphozoan medusae and pelagic tunicates that are more robust and can be collected via trawling, siphonophore colonies often break apart in trawl samples and are therefore difficult to obtain intact. Yet they may serve as important trophic roles in the jelly web, linking zooplankton to higher trophic level taxa (Choy et al. 2017). Siphonophores have broad geographic and vertical distributions, with surface-dwelling, midwater, and benthic species, and they are abundant predators in global zooplankton communities (Mackie et al. 1988; Haddock et al. 2005; Choy et al. 2017).

In marine ecosystems, predator–prey relationships are typically size-based, where prey are predictably smaller than their predators (Wirtz 2012). Siphonophores challenge size-based theoretical assumptions of predator–prey interactions because colony size is not a reliable indicator of potential prey size. Siphonophores are composed of multiple zooids and bear numerous feeding structures along the lengths of their bodies (Pagès and Madin 2010, Wirtz 2012; Fig. 1). Unlike a coral colony, where the polyp zooids are functionally equivalent, siphonophore zooids are highly specialized to carry out specific functions (Fig. 1). Gastrozooids are feeding polyps that bear a mouth and digestive tissues (Mapstone 2014). Gastrozooids have a single, long tentacle with side branches (tentilla), which are used to capture and subdue prey (Mapstone 2014). Tentilla morphology is highly diverse across species (Damian-Serrano et al. 2021b). Since tentilla are exclusively used for feeding, morphological variations may reflect niche partitioning and interspecific diet specialization (Damian-Serrano et al. 2021a). Because of their distinct and diverse morphology and their presence across depth habitats, siphonophores may occupy numerous trophic niches in pelagic ecosystems.

Synthesizing current knowledge of siphonophore predator–prey interactions is timely, as recent developments and advances in oceanographic sampling and analytical approaches (e.g., plankton imaging systems, molecular techniques, biochemical tracers) allow for more detailed analyses of fragile and cryptic taxa. Our overarching objective was to examine the roles of siphonophores in marine food webs by quantifying their predator–prey relationships reported in the literature. To address this objective, we asked the following questions: (1) What are the trophic roles of siphonophores in pelagic food webs? (2) Do siphonophore feeding niches differ between epi- and deep-pelagic habitats? We demonstrate an improved understanding of the ecological roles of siphonophores their contributions to pelagic food webs. Based on our findings, we discuss how contemporary methods can further our understanding of siphonophore trophic ecology and present directions for future research.

Methods

We conducted an extensive *Web of Science* literature review (March 2020) to identify and collate published siphonophore papers from 1960–2020. The terms siphonophor*, or cystonect*, or calycophor*, or physonect*, were used to search all titles and abstracts in *Web of Science* databases for the appropriate literature. Asterisks were used to include groups of characters, for example, cystonect* returns searches matching cystonect, cystonects, Cystonectae. From the initial results, we removed duplicates (e.g., papers and their supplementary material listed separately), non-peer-reviewed results (e.g., student theses, government reports), data repositories, and non-English publications. We then sorted publications into six broad categories: abundance/distribution, general biology, taxonomic descriptions, evolution/phylogeny, trophic ecology/diets, and other for publications outside the scope of those categories. To compare the number of siphonophore publications with those on other GZ, we searched for

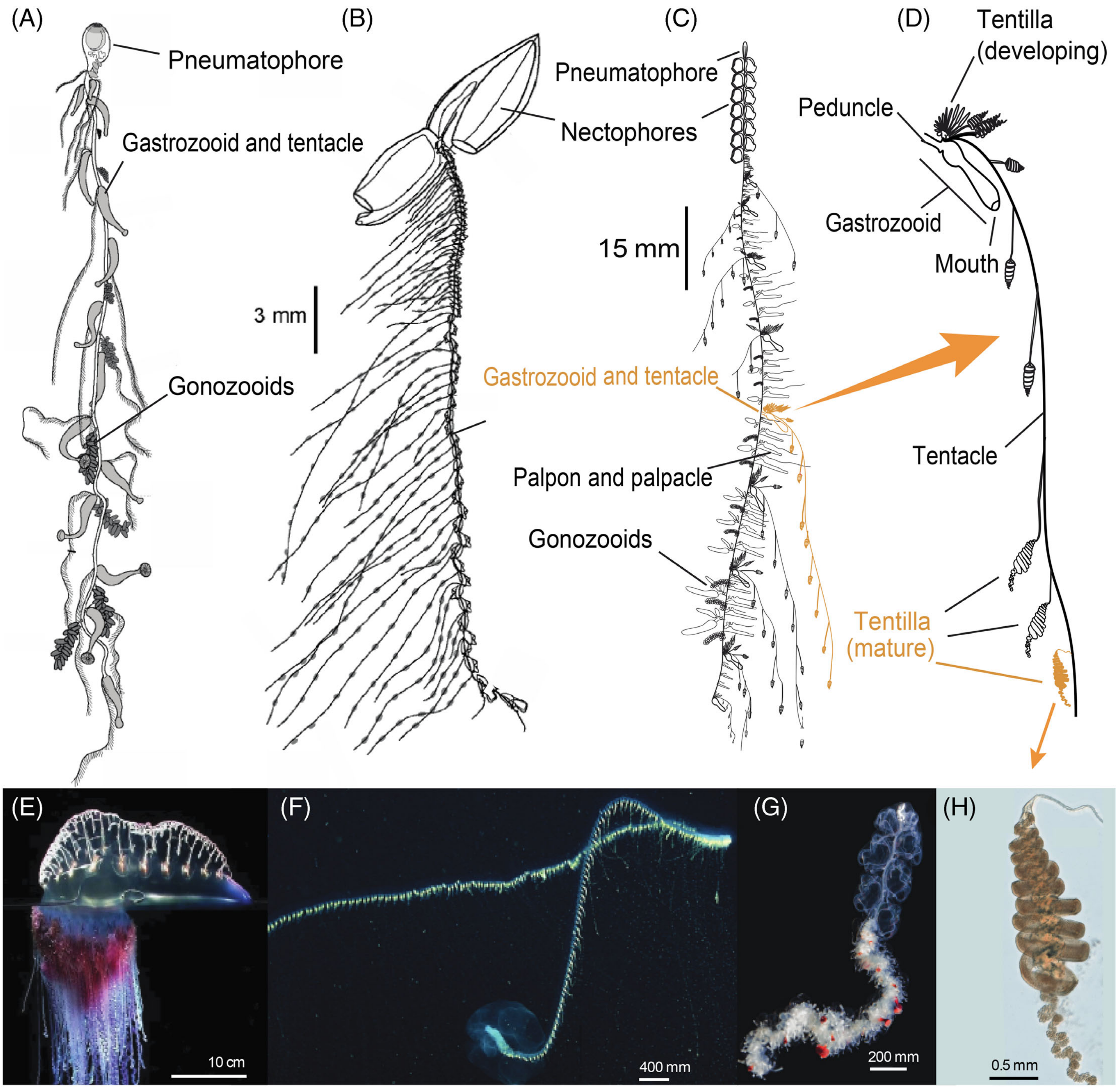

Fig. 1. Illustrations and images of siphonophore body plans from each suborder, (**A**) the long-stemmed cystonect *Rhizophysa eysenhardtii*, (**B**) calycophoran *Lensia conoidea*, (**C** and **D**) illustration of a *Nanomia* sp. colony, gastrozooid, and tentacle (illustration by Freya Goetz), (**E**) the cystonect *Physalia physalis* with enlarged pneumatophore (photo by Casey Dunn), (**F**) *Praya dubia* (Photo Monterey Bay Aquarium Research Institute), (**G**) *Apolemia lanosa* (photo by Stefan Siebert), and (**H**) transmission micrograph of a tentillum of *Nanomia* sp. (by Alejandro Damian-Serrano).

publications on other gelatinous taxa using the following terms: jellyfish*, cnidaria*, tunicat*, and ctenophor*.

We used all siphonophore predator–prey interactions that were found in the literature to create a network of purported trophic interactions. These predator–prey interactions were obtained from various sampling and analytical techniques, each with distinct biases (*see* "Methodological advancements" section). Some reports were anecdotal or based on small numbers of observations. These observations were used to create a food web diagram but not to test for diet differences between siphonophore suborders. A small subset ($n = 3$) of reported studies contained quantitative diet data (Purcell 1981a, 1984a, b, and Choy et al. 2017), and those datasets alone were used for quantitative analyses. For data from gut contents analysis (GCA), the number of colonies and gastrozooids per colony analyzed varied among species and studies. We used the relative percentages of prey reported for each siphonophore specimen.

From the quantitative diet data, we evaluated differences in siphonophore diet between each suborder. One study reported siphonophore diets in relation to ambient prey communities (Purcell 1981a). For species in Purcell (1981a) we calculated prey selectivity between siphonophore species using Ivlev's Electivity index (Ivlev 1961) for each species (also presented in Damian-Serrano et al. 2021a), where E_i is electivity, r_i is the relative abundance of a prey in a predator's diet and P_i is the prey's relative abundance in the ambient environment. Values range from -1 to 1, where 1 indicates an exclusive preference for prey and -1 indicates total avoidance. We refer to this index as selectivity, although we note that it can also reflect prey vulnerability to predation rather than active prey selection. Taxon-specific selectivity was calculated for the following prey: copepods, amphipods, decapod larvae, ostracods, shrimp, chaetognaths, fishes, mollusks, gelatinous animals, and other.

From the quantitative and qualitative siphonophore-prey interactions we created topological species interaction networks for both the epipelagic and deep-pelagic datasets using the package "bipartite" and function *networklevel* in R (Dormann et al. 2008). Since predation on siphonophores is poorly documented in the literature and bipartite networks were used, predator-siphonophore interactions were not included. Networks were created using either siphonophore species-specific (or the lowest taxonomic ID) data or data where siphonophore-prey interactions were binned by siphonophore suborder. Thus, we compared four networks: (1) epipelagic + suborder, (2) epipelagic + species-specific, (3) deep pelagic + suborder, (4) deep pelagic + species-specific. Within these networks, we examined the effects of species-specific interaction data and depth habitat on network structure, measured by five food-web parameters: (1) weighted Nestedness based on Overlap and Decreasing Fill (NODF): a nestedness metric where higher values indicate higher nestedness, (2) weighted connectance: linkage density divided by the number of species in the network, used to measure network complexity, (3) Shannon diversity: taxonomic diversity and evenness of interactions, (4) linkage density: total weighted diversity of interactions per species, and (5) specialization (H2), which describes the specialization or selectivity of a bipartite network. Values range between 0 (no specialization; opportunistic) and 1 (single-taxon specialization) and represent deviations from expected interactions given the total number of species on the network (Blüthgen et al. 2006). H2 is therefore defined relative to the minimum and maximum numbers of interactions in a network.

To test for the robustness of these results to taxon subsampling and to correct for differences in the number of taxa between food-web representations, we carried out bootstrapped *t*-tests. For each contrast, we drew 100 subsamples of *N* interactions from the largest among the two food webs compared, where *N* is the total number of interactions in the smallest of the two food webs. Then, we calculated the topological parameters (1)–(5) for each subsample and ran one-tailed *t*-tests contrasting the bootstrapped distributions of each parameter to the values estimated for the smallest web.

Results and discussion

The literature review shows that siphonophores are understudied compared to other gelatinous taxa, with a paucity of publications on siphonophore food-web interactions (Figs. S1, S2). We found a total of 449 publications on siphonophores in the *Web of Science* query, with 37.3% focused on siphonophore distribution, 28.3% on species or taxonomic descriptions, and only 19 studies (4%) focused on diet or trophic ecology (Fig. S2). We compiled 285 predator–prey interactions where siphonophores were predators and 58 interactions where siphonophores were prey (Fig. 2). There were documented feeding interactions for at least 17 calycophoran, 5 cystonect, and 19 physonect species spanning epipelagic to bathypelagic depths (Tables S1, S2). In some studies, siphonophores were identified only to a broader taxonomic level (e.g., suborder, family, or genus) so the reported species number is likely underestimated.

Siphonophore food-web interactions

Siphonophores as predators

Prey eaten by siphonophores span multiple trophic levels and functional groups. Prey included various crustaceans (copepods, crab zoeae and megalopae, ostracods, stomatopods, shrimps), chaetognaths, mollusks (heteropods, pteropods, veliger larvae), fish (adults, juveniles, and larvae), and other GZ (siphonophores, ctenophores, narcomedusae, trachymedusae, tunicates) (Figs. 2, 3). These results are supported by Chi et al. (2021), which used nitrogen and carbon isotope analysis on the primary components of the jelly web (scyphomedusae, pelagic tunicates, siphonophores, ctenophores). Their results suggest that GZ have diverse functional roles in the food web, with isotopic niche space covering 3–4 trophic levels. Specifically, in line with our results, stable isotope values also suggested that siphonophores occupy several trophic levels. Further, our synthesis of siphonophore predation supports other recent work illustrating that GZ do not represent a single functional group within food webs, but rather they occupy numerous trophic roles (e.g., Choy et al. 2017; Hays et al. 2018).

60.3% of all siphonophore species predation events were on crustaceans, followed by 11.6% on fish, while cnidarians, mollusks, chaetognaths, ctenophores, tunicates, and

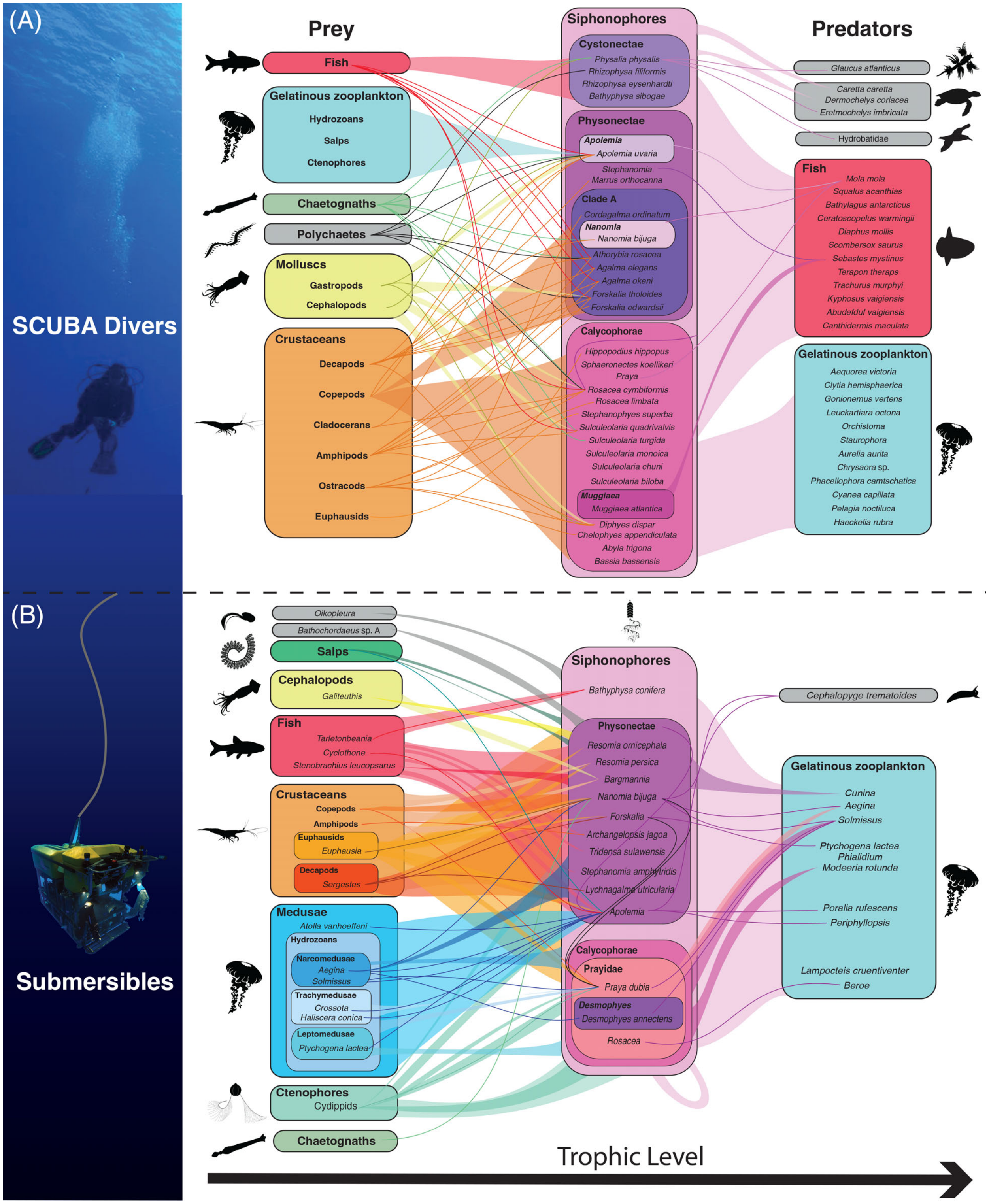

Fig. 2. Siphonophore predator–prey relationships from previously published diet studies, where siphonophore prey are in the left column and predators are on the right. (**A**) Analysis of gut contents of siphonophores collected via blue-water diving, DNA studies, and anecdotal observations and (**B**) interactions observed using submersibles. Specific interactions are depicted as nested within broad group interactions. *See* Tables S1, S2 for predator–prey interaction data.

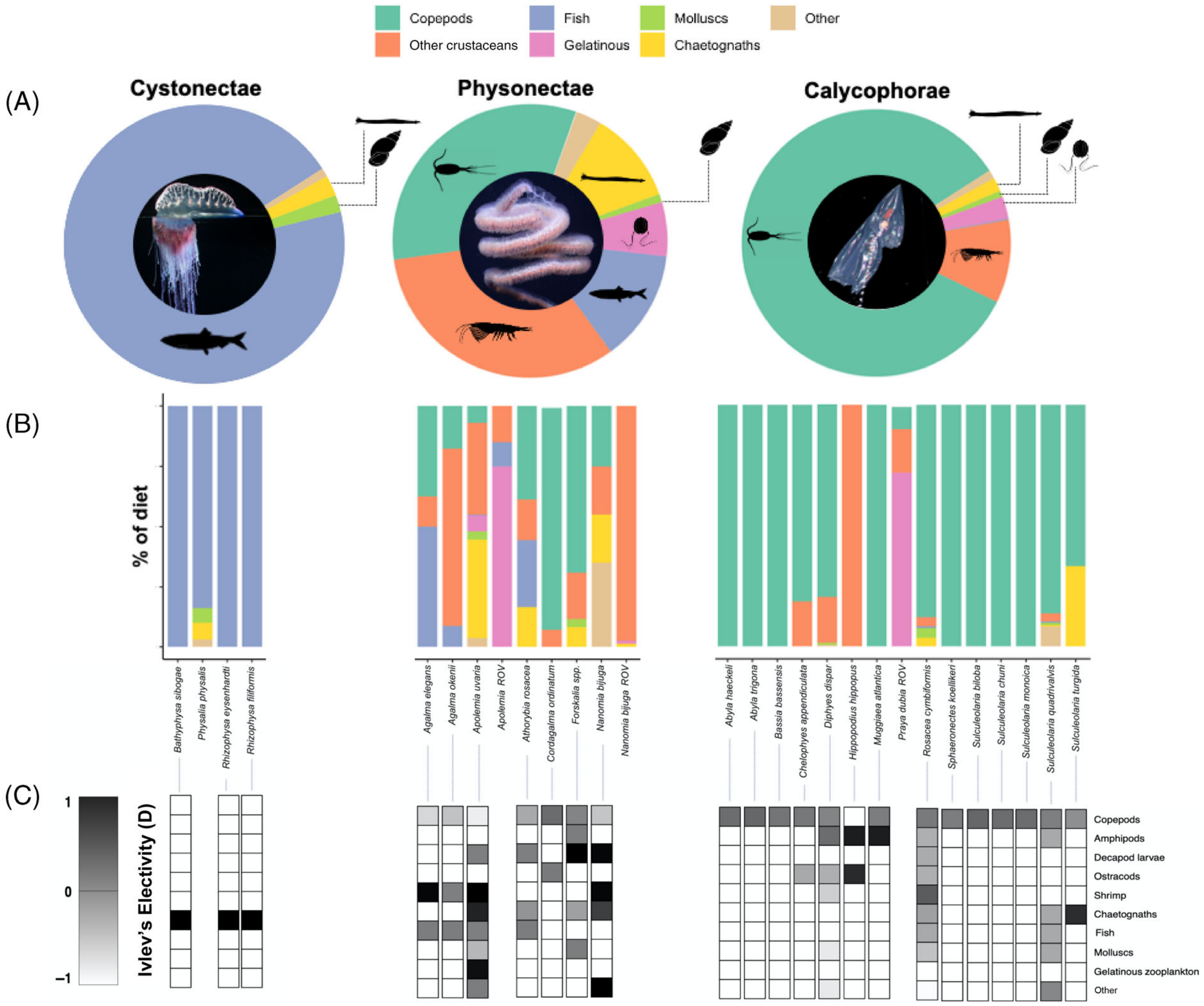

Fig. 3. (**A**) Relative contributions (%) of prey taxa to the diets of siphonophore suborders (Calycophorae, Cystonectae, and Physonectae), (**B**) species-specific siphonophore diet contributions (%), where predator–prey data for A and B were compiled from gut contents analysis (Purcell 1981a, 1984a,b) and ROV data (Choy et al. 2017) for species with > 10 feeding observations. (**C**) Ivlev's electivity index, scaled from − 1 (white; indicating total exclusion of prey) to 1 (black; indicating exclusive enrichment). Prey and prey field composition data were derived from Purcell 1981a and taxon-specific electivity was calculated for each siphonophore species.

polychaetes all comprised smaller diet proportions. When data were analyzed separately for each suborder, calycophoran diets were heavily dominated by crustaceans (73.7%), with no other taxa individually comprising > 10% of their diets (Fig. 3A). Physonect species primarily preyed on crustaceans (58.4%), but to a lesser extent than calycophorans, while fishes (12.0%) and cnidarians (7.0%) comprised more substantial proportions of physonect diets. Cystonects relied the least on crustaceans, with diets heavily dominated by fish (75.0%), followed by mollusks (12.5%).

Data from previous studies indicate that many siphonophore species are specialized and selective, although some species' diets were variable, suggesting more generalist feeding behavior. For example, Purcell (1981b) reported that copepods were the most dominant prey for *Rosacea cymbiformis*, but there were many other taxa that appeared in their diets, albeit less frequently. Similarly, *Physalia physalis* primarily consumes fish, but has also been documented consuming other fast-swimming, soft-bodied prey like cephalopods and chaetognaths (Purcell 1984b), possibly when their preferred prey are not abundant. In the mesopelagic, selective feeding behavior has been documented for *Nanomia bijuga*, where Choy et al. (2017) observed 72 *N. bijuga* feeding interactions (mean depth = 277 m) in which euphausiids were their dominant prey. Similarly, in the Gulf of California, Purcell (1981c) reported that 100% of the gut contents of *Rhizophysa eysenhardtii* were fish larvae. This study also showed a clear difference between the proportion of fish larvae in the gastrozooids relative to their abundance in the water column, suggesting strong selectivity. Additionally, feeding occurred primarily during the day although fish larvae were equally abundant at night. Combined with the presence of fluorescent tentacle tips (Haddock and Dunn 2015) this suggested that *R. eysenhardtii* was using ambient light to excite lures and attract its prey.

Only one of the reviewed studies (Purcell 1981a) examined siphonophore feeding interactions in the context of the prey community. For the subset of data where diet and ambient prey communities were quantified, Ivlev's electivity index showed strong selectivity by cystonects for fish and varying degrees of selectivity by calycophorans for copepods (Fig. 3). Physonects were generally species-specific predators and different species showed varying selectivity for numerous prey types (e.g., copepods, ostracods, chaetognaths, fish) (Fig. 3). Selectivity was also species-specific, with some species showing strong preferences for one prey type (e.g., *R. eysenhardtii*) and others (e.g., *Sulculeolaria turgida*) exhibiting more generalist behavior. However, our analyses were restricted to a limited dataset, and future studies that simultaneously evaluate predator and prey abundances are needed to test hypotheses about diet specialization, particularly for deep pelagic species.

When we compared feeding networks, differences between interactions in the epipelagic and the deep pelagic were evident, as well as between species and suborders (Figs. 4, 5). Notably, H2 (specialization), was 0.52 in the deep species-specific network, which was significantly higher than the epipelagic network (0.20, bootstrap *p*-value <0.0001), suggesting that siphonophore feeding interactions in the deep pelagic are more specialized compared to the epipelagic. As expected by the more inclusive taxonomy, this trend was less pronounced when suborder level rather than species-specific data were used. Further, the weighted NODF (nestedness) was lower in the deep pelagic (12.9) compared to the epipelagic (26.3,

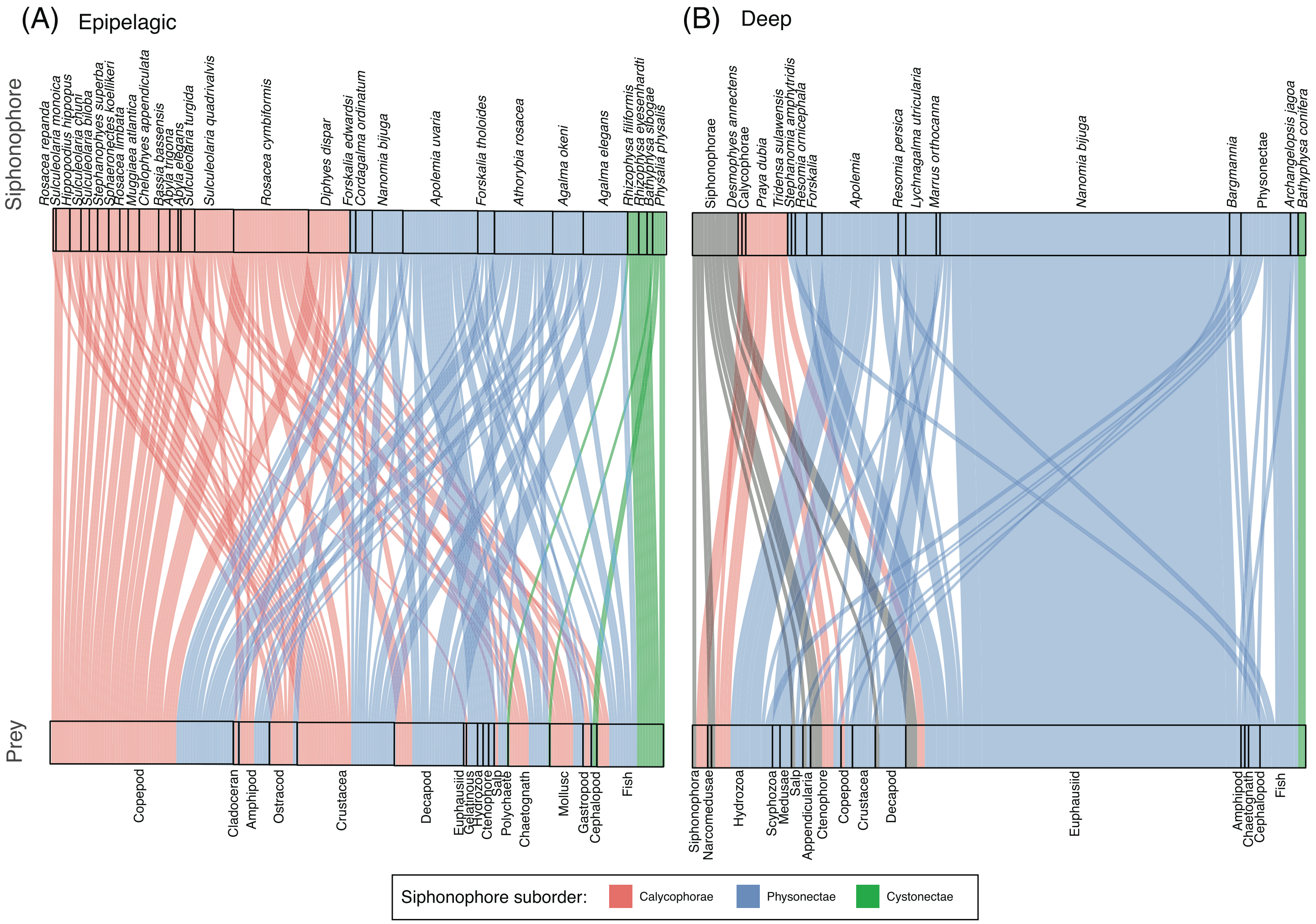

Fig. 4. Predator–prey network topology in (**A**) epipelagic and (**B**) deep-pelagic habitats between siphonophores and their prey. Data on epipelagic interactions are mainly from Purcell (1981a) and deep-pelagic interactions are mainly from Choy et al. (2017) but include all siphonophore-prey interactions that were used to generate Fig. 2. *See* Tables S1, S2 for predator–prey interaction data.

Fig. 5. Heatmap of network topology parameters, comparing epipelagic and deep-pelagic networks with either species-specific (or lowest taxonomic ID) siphonophore predator–prey interactions or with species binned into three siphonophore suborders (*see* Fig. 4). Color indicates normalized deviations from the mean for each parameter and numbers are raw values for each parameter. Network topology parameters are: (1) weighted NODF to measure nestedness where higher values indicate nestedness, (2) weighted connectance, which is linkage density divided by the number of species in the network, (3) Shannon diversity, which measure taxonomic diversity and evenness of interactions, (4) linkage density, which measures the total weighted diversity of interactions per species, and (5) H2, or specialization, which ranges between 0 (no specialization) and 1 (complete specialization). Data on epipelagic interactions are mainly from Purcell (1981a) and deep-pelagic interactions are mainly from Choy et al. (2017) but include all siphonophore-prey interactions (*see* Table S1).

bootstrap p-value <0.0001; Fig. 5). The bootstrap random subsampling t-tests show strong support for all parametric differences found between network comparisons.

These results suggest that siphonophore predator–prey interactions in the deep pelagic are not nested and specialists' diets are unique contributions to the food web's complexity, rather than a redundant subset of generalist diets. It is possible that specialization is reflective of the scarcity of resources in the deep pelagic. Deep pelagic siphonophore species may carve out distinct ecological niches to coexist and avoid competitive exclusion. The network comparisons demonstrate the importance of species-specific data, where many physonect species in the deep pelagic specialize on different prey types. Calycophorans predominantly prey on copepods and other small crustaceans but physonect diets were more varied and species-specific. Thus, specialization is obscured when diet data are analyzed with siphonophore data binned by suborder. Higher specialization in the deep networks may suggest differences in food web structure between habitats, which has implications for how energy flows through the jelly web. Recently, Chi et al. (2021) also found that GZ in deeper habitats (400–1000 m) exhibited more isotopic niche partitioning compared to shallow habitats, which may support findings from our network analysis.

Although our network analyses indicated more specialization in the deep pelagic (Higher H2 values; Figs. 4, 5), these findings may reflect differences in sampling methodology (GCA vs. ROV data) between epi- and deep-pelagic studies, rather than ecological differences between shallow and deep species. Due to the scarcity of siphonophore-prey diet data, our sampling design was unbalanced, where siphonophore species and the number of observations were not constant across depth habitats. Future work is needed to collect quantitative diet data on the same species across depths habitats using one methodology to examine potential differences in siphonophore niches between the epi- and deep-pelagic (*see* "Potential caveats and current limitations" section).

Intraguild predation and "the jelly web"

Intraguild predation between soft-bodied organisms remains particularly poorly resolved in pelagic food webs due to the difficulties in detecting their trophic interactions (Arai 2005). There is evidence that intraguild predation is common in the jelly web (Arai 2005). However, diet studies of epipelagic siphonophore species (Purcell 1981a, 1991; Purcell and Arai 2001) have shown little evidence of predation on GZ, and no siphonophore species is known to exclusively consume GZ. For example, Purcell (1981a) found that hydromedusae and ctenophores only constituted 1% of siphonophore prey, except for *Apolemia* sp. which consumed 13.3% GZ. Few publications report siphonophores consuming GZ, but this may reflect the inability to detect predation on soft-bodied prey using traditional methods like GCA.

Choy et al. (2017) presented mesopelagic food web structure from remotely operated vehicle (ROV) observations and reported numerous siphonophore interactions with other GZ. For example, they observed the hydrozoan *Solmissus* spp. preying on calycophorans and physonects. Several observations were made of siphonophore feeding, particularly of *Praya dubia*, consuming other siphonophores (*N. bijuga* and *Forskalia* spp.). It is possible that study-specific discrepancies in sampling methodology could reflect diet differences between epipelagic and mesopelagic siphonophores. It is also possible that intra-siphonophore predation has not been reported in epipelagic species because studies have relied on GCA, which underestimates gelatinous components of predator diets (Hays et al. 2018).

Siphonophores as prey and other ecological interactions

In contrast to the mounting evidence that GZ are generally important prey for higher trophic levels, there are few reports of predators specifically consuming siphonophores. Consumption of siphonophores is likely difficult to detect as they are transparent, lack hard parts and are quickly degraded and digested in the guts of consumers. Siphonophores also have low nutritional content and bear stinging nematocysts which deters predation. It is possible that predation on siphonophores is high but rarely observed. Some studies on the diets of higher trophic level species group all GZ together, as they are unable to identify specimens to a more precise taxonomic level (e.g., Hays et al. 2018). These factors likely lead to an underestimation of reports of predation on siphonophores. The few interactions reported in the literature are likely biased toward conspicuous and surface-dwelling species (e.g., seabirds consuming *P. physalis*, Pitman and Ballance 1990).

There are reports of several fish, turtle, and seabird species consuming siphonophores. Some of these reports are anecdotal, rather than quantitative. Of the 58 predator–prey interactions, we found where siphonophores were prey, only 21 identified siphonophores to the genus or species level, where the remainder were identified to the suborder or order. Three marine turtle species, two of which are of critical conservation concern, have been documented consuming siphonophores (Van Nierop and Hartog 1984; Stampar et al. 2007). Siphonophores also have invertebrate predators, including amphipods (Gasca and Haddock 2004), mollusks, scyphozoans (Purcell 1991), ctenophores, and other siphonophores (Purcell 1991; Choy et al. 2017). For example, Choy et al. (2017) reported *P. dubia* consuming a physonect siphonophore from the genus *Forskalia*. This has also been shown for the sunfish *Mola mola*, where animal-borne cameras revealed predation on three siphonophore genera (Nakamura et al. 2015), and DNA barcoding identified predation on *Physophora hydrostatica* (Sousa et al. 2016). A study of gelativory in the giant “seven-armed octopus” *Haliphron atlanticus* (Hoving and Haddock 2017) included gut contents identifiable as a physonect siphonophore. These recent studies underscore the potential for more recently developed techniques to identify previously undetected trophic linkages in food-web studies.

While our primary focus was on predator–prey interactions, several studies have noted additional ecological roles of certain siphonophore species such as providing shelter, protection, and potentially resources to other species. For example, Purcell (1984b) documented the association between fish and *P. physalis*, and Robison (1983) observed that the fish *Leuroglossus stilbius* fed on crustaceans on the tentacles of *Apolemia* spp. Siphonophores also act as hosts for many hyperiid amphipods; several *Phronima* species make a nest for their young in the nectophores of *Sulculeolaria*, *Nanomia*, *Vogtia*, and *Abylopsis* species (Laval 1980, pers. obs.). Lastly, siphonophores are often used as substrates by palinurid phyllosoma larvae (Ates et al. 2007). These interactions are not well understood, and net tow sampling disrupts these biological associations (Gasca and Haddock 2004). Future in situ studies from ROV and AUV footage will be particularly useful for detecting these behaviors and ecological interactions.

Potential caveats and current limitations

This review presents the first synthesis of all published siphonophore feeding interactions but is based on a small number of studies. Of the 19 studies on siphonophore trophic interactions, only three contained quantitative diet data. We emphasize that there are many siphonophores species for which there are no published diet or trophic interaction data. Due to the paucity of data on siphonophore feeding interactions, data used for this synthesis were collected at different times and sampling locations (Fig. S1) and relied on different collection methodologies. Data were almost exclusively limited to the Northern Hemisphere, particularly in the northeastern Pacific and North Atlantic Ocean (Fig. S1). Quantitative data were derived from samples collected in different ecosystems, including the Gulf of California, the California Current, and the Sargasso Sea. These regions have distinct productivity and oceanography, which may affect predator diets. While we were unable to perform inter-ecosystem comparisons in siphonophore feeding ecology, we recognize that intraspecific differences in diet between ecosystems and time periods may exist.

Most diet data from individual siphonophore species were derived from only one method, primarily either GCA or ROV videos so it was not possible to disentangle ecological vs. methodological differences between depth habitats. *N. bijuga*, *Apolemia* spp., and *Forskalia* spp. were the only siphonophores for which there was diet data derived from two sources, GCA (Purcell 1981a) and ROV observations (Choy et al. 2017). We were unable to test for statistical differences between diet data derived from the two methods, but there were diet discrepancies between methods for both species. *Apolemia* spp. diets derived from GCA were more diverse than *Apolemia* spp. predation observed by ROVs. Prey from GCA were primarily chaetognaths and crustaceans, whereas ROV observations indicated *Apolemia* spp. primarily consumed gelatinous prey and to a lesser extent, fish and crustaceans. This difference could be driven by gelatinous prey not being preserved in gastrozooids. Observations also included several apolemiid species, some of which are cryptic and undescribed, which could have contributed to diet differences between the two studies. Similarly, *Forskalia* spp. in the mesopelagic has been observed feeding on euphausiids and decapod crustaceans, while

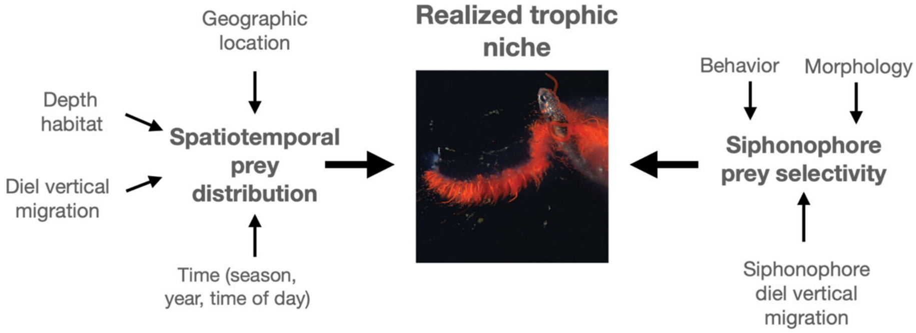

Fig. 6. A conceptual framework summarizing likely drivers of siphonophore trophic ecology that have been suggested in the literature: The composition and abundance of ambient prey communities which varies across spatiotemporal scales, depth habitat, and the diel vertical migration patterns of both siphonophores and their prey. Siphonophores are also selective predators, where prey selectivity is influenced by behavior (e.g., swimming posture) and morphology (e.g., tentillum and nematocyst morphology varies between species). Photo credit: Choy et al. (2017).

Biggs (1977) identified fish, amphipods, and mollusks, in addition to crustaceans, in the guts of the epipelagic species *F. tholoides* and *F. edwardsii*. However, there were only four total ROV observations of *Forskalia* spp. and they were identified to genus.

For *N. bijuga*, GCA identified chaetognaths, copepods, shrimp, and decapod larvae as prey, whereas ROV videos indicated *N. bijuga* almost exclusively prey on euphausiids. These differences may be attributed to collection depths: specimens collected for GCA were from < 30 m, whereas ROV observations were from the mesopelagic. The differences in *N. bijuga* diet between studies may support findings from our network analyses suggesting that siphonophore-prey interactions in deep pelagic habitats are more specialized. These qualitative discrepancies underscore the need for more comparative studies of siphonophore diets across depth habitats, ecosystems, and using consistent methodological approaches.

Potential drivers of siphonophore diet

Our results suggest differences in feeding niches between epi- and deep-pelagic species. However, the factors that explain variation in siphonophore diets remain unknown. From the literature review, we summarized several likely drivers of siphonophore trophic ecology (Fig. 6). In pelagic ecosystems, community density and composition—and therefore available prey—varies horizontally, vertically, and temporally and is driven by various physical and biological factors (Sommer et al. 2017; Netburn and Koslow 2018; Thompson et al. 2019). This variability is likely to influence siphonophore feeding interactions. In epipelagic siphonophores, Purcell (1981a) showed that the number of prey items in siphonophore guts was typically correlated with the available prey community and was also influenced by time of day and the amount of sunlight. It is unclear whether these relationships also exist for deep pelagic or specialized species.

Functional morphology likely plays an important role in determining siphonophore diets. Some siphonophores have evolved unique traits to aid in attracting or capturing prey, including the use of lures or mimicry behavior (Purcell 1980; Haddock et al. 2005; Pugh and Haddock 2010; Haddock and Dunn 2015; Pugh and Haddock 2016). These adaptations are used to attract different taxa and demonstrate the specialization for siphonophores feeding in midwater communities. Recent work (Damian-Serrano et al. 2021a,2021b) hypothesized that tentillum morphology may be a useful predictor for siphonophore diets, particularly to distinguish between generalist and specialist species. For example, siphonophores that specialize on copepods have convergently evolved smaller tentilla with fewer and smaller nematocysts (e.g., *Hippopodius hippopus*, *Diphyes dispar*, *Chelophyes appendiculata*, *Sulculeolaria quadrivalis*) compared to species that prey on other taxa.

The number of prey that siphonophores can capture and digest is likely also dependent on prey type and size, where handling time may vary across prey taxa. The size of a siphonophore's gastrozooid may limit the range of prey sizes that siphonophores can capture. Early studies hypothesized that species with small gastrozooids primarily consume small crustaceans (e.g., copepods), whereas species with larger gastrozooids have more variable diets and can consume a wider range of prey taxa or specialize on larger prey (Purcell 1981a). However, recent studies have shown that some siphonophores can ingest prey that are larger than their gastrozooids (e.g., *Halistemma cupulifera* consuming leptocephalus larvae; Pagès and Madin 2010). Using stable isotope analysis, Chi et al. (2021) found no relationship between nitrogen isotope values (a proxy for trophic position) and nectophore (swimming bells) size. The relationship between zooid size and prey size is uncertain and may differ between shallow and deeper-dwelling species, highlighting the need for further research.

Methodological advancements in siphonophore collection and dietary analysis

Studying the biology and trophic ecology of GZ has traditionally been limited by our abilities to effectively sample fragile taxa. Recent advances in our ability to collect siphonophores and analyze their trophic interactions now facilitate studies on siphonophore food web interactions. While trawling remains the most common technique for collecting zooplankton and micronekton, it often destroys fragile gelatinous animals (Table S3). Trawl systems can be modified to minimize damage to animals, which can reduce the sampling bias against GZ. For example, towing nets slowly and using specialized cod-ends (i.e., thermally-insulated; Childress et al. 1978) can increase the success of capturing siphonophores (Raskoff et al. 2003). Traditionally, blue water SCUBA diving has been the primary mode of collecting fragile GZ (Biggs 1977; Table S3) but it is limited by personnel, depth (i.e., epipelagic species), and diving conditions (Raskoff et al. 2003; Haddock and Heine 2005).

Advances in the development of submersibles and ROVs have been instrumental in collecting and observing deeper-dwelling siphonophores. Submersibles can be equipped with large collection cylinders that allow for the collection of specimens with minimal damage and camera systems that capture in situ observations (Choy et al. 2017; Pugh et al. 2018; Robison et al. 2020). Robison et al. (1998) used ROV observations to estimate the depth distribution of *N. bijuga* and describe temporal variation in its abundance in relation to surface primary production. ROVs can also capture trophic interactions between fragile taxa, including siphonophores (Robison et al. 1998; Choy et al. 2017). While ROVs have certainly advanced our sampling capabilities, they are limited by cost, highly-trained personnel, collection capacity (number of collection cylinders/chambers). ROVs may also underestimate small prey or fast-moving prey that are deterred by bright lights. Further, diets inferred from ROV videos are based on a relatively small number of in situ feeding interactions.

Autonomous vehicles equipped with imaging systems have increased our capacity to study siphonophores. One such example is the *ZooGlider*, which is an autonomous zooplankton imaging system that can be deployed for up to 50 d and can image from the surface to 400 m depth (Ohman et al. 2019). Towed imaging systems also exist, such as the In-Situ Ichthyoplankton Imaging System (ISIIS; Cowen and Guigand 2008) or the Pelagic In situ Observation System (PELAGIOS; Hoving et al. 2019), which can record high-resolution images and collect environmental data. While these techniques do not have the capability to collect specimens for further analyses, the data they produce can provide essential information about the abundance (e.g., Briseño-Avena et al. 2020), density, functional morphology, and behaviors of siphonophores and ambient prey communities.

Seminal studies on siphonophore diets (Biggs 1977; Purcell 1981a) relied on GCA and examining the contents of gastrozooids from a colony. This approach provides the most direct taxonomic information on consumer diets and has been widely used to study food-web relationships for at least a century (Lea and Gray 1935; Olson and Boggs 1986; Fry 2006). While GCA often provides the taxonomic identity of ingested prey, it offers a dietary snapshot rather than dietary information integrated over time. Further, GCA is biased toward hard-bodied taxa and is limited by taxonomic expertise, time, and high sample size requirements, as some collected specimens have empty guts.

Biochemical techniques such as fatty acid and stable isotope analyses have become widely-used approaches to complement GCA in ecological studies (Nielsen et al. 2018; Parzanini et al. 2019). Stable isotope values can provide trophic position estimates of siphonophores, and information about the trophic structure of zooplankton communities independent of GCA. The main limitation of both stable isotope and fatty acid analysis is they do not provide precise taxonomic identification of prey species. These techniques are therefore most effective when there is a priori knowledge of the consumer's diet (Syväranta et al. 2012). In the few studies where siphonophore isotope values have been determined (e.g., Fanelli et al. 2011; Tilves et al. 2018), siphonophores were not the primary focus of the study. Other studies may include siphonophores but group all GZ together or include siphonophores in broader groupings of zooplankton communities. We recognize that these studies may not be reflected in our literature review, as we focused on studies that provided siphonophore-specific trophic interactions.

More recently, DNA techniques have been used in diet studies for taxonomic identification of gut contents through amplicon sequencing of gene fragments from ingested prey (Nielsen et al. 2018). Molecular tools have not yet been used to estimate siphonophore diets but could complement stable isotope analyses by providing taxonomic identifications of prey. This is particularly advantageous for the study of deep-pelagic predators, which sporadically capture prey over time intervals that exceed digestion times. While these approaches provide a taxonomic identification of prey species, they are not quantitative and cannot distinguish ecologically distinct yet genetically identical life cycle stages of prey, secondary predation, or cannibalism.

A vision for future research

This review shows that siphonophores are central members of the "jelly web" and through their roles as predators and prey, they transfer energy through numerous pathways in pelagic ecosystems. We emphasize that siphonophores are understudied components of marine ecosystems. With new technologies that can better capture these fragile animals, and contemporary methodologies to identify predator diets, we are better suited to expand our knowledge on the ecological roles of siphonophores and quantify energy transferred through the "jelly web." Based on our findings, we identify major gaps in our understanding of the trophic roles of siphonophores and provide a framework for future research.

Network analyses indicated potential differences in dietary niches between epi- and deep-pelagic siphonophores but it is unclear if these findings reflect ecological or methodological differences. Future studies are needed to disentangle these confounding factors. To compare siphonophore diets across depth habitats, it is necessary to co-collect diet data from the same species using consistent methodology. It is also important to compare diet data derived from different methodologies to quantify specific biases associated with each methodology.

While the literature suggests several potential drivers of siphonophore diets (i.e., morphology, behavior, and community composition of ambient prey communities), these factors have mostly been considered qualitatively and in a small number of siphonophore species, primarily restricted to the epipelagic. Further, the extent to which each of these factors contributes to the variation in siphonophore diets remains unresolved. Future studies that quantify siphonophore diets from more species that vary in morphology and depth habitat would allow us to test hypotheses about variations in siphonophore ecological niches.

As discussed above, integrating biochemical markers or molecular tools into future studies will be useful for identifying siphonophore-prey relationships. This is evidenced by recent work (Chi et al. 2021) demonstrating the large potential for stable isotope analyses in studies focused on GZ trophic interactions. Further, trophic position estimates derived from stable isotope analysis can be used in ecosystem or food-web models, which often do not account for, or oversimplify, the GZ component (Pauly et al. 2008; Chi et al. 2021). Although metabarcoding has not been used in siphonophores, metabarcoding of higher trophic level predators has revealed that GZ are common prey for higher trophic level species (Lamb et al. 2017) and specifically, siphonophores are prey (Sousa et al. 2016). These techniques have large potential to advance our understanding of siphonophore trophic ecology, particularly for deep-sea specimens that are more difficult to collect for GCA, and to identify gelatinous diet items that are not detected by GCA.

Tunicate gelatinous taxa (e.g., salps, pyrosomes, and larvaceans) play important roles in marine geochemical cycles, transferring large amounts of carbon from the surface to the deep ocean during large blooms (Henschke et al. 2016), but there are few estimates of spatiotemporal siphonophore abundance (Robison et al. 1998; Silguero and Robison 2000; Briseño-Avena et al. 2020). Siphonophore blooms have been reported (Greve 1994) but the extent and ecological impact of these bloom events are largely unknown. For a more complete picture of how siphonophores contribute to carbon flow and food web dynamics, future studies are needed to estimate siphonophore abundance and depth distributions. Abundance estimates of siphonophores would be particularly useful contributions to food-web models.

Although siphonophores are known to undertake vertical migrations (Pugh 1984; Mackie et al. 1988), diel depth distributions are not available for many species, and it is unclear to what degree siphonophores link surface and deep-pelagic communities through trophic interactions. Future studies that describe siphonophore depth distributions and vertical migration patterns are needed to address questions about connectivity. In situ videos and images will be particularly useful complements to trawl data for quantifying siphonophore abundances with depth.

Coupled with data on vertical distributions, work on siphonophore predator–prey abundance, overlap, and siphonophore predation rates would greatly advance our ability to estimate predation and competition impacts of siphonophores on zooplankton communities. One study (Purcell 1984b) estimated that *P. physalis* colonies may be a considerable cause of local larval fish mortality, with individual colonies consuming ~ 120 larval fish per day. Aside from a select number of epipelagic species, the predation impacts of siphonophores remain largely unknown. These studies require co-collection of siphonophores and their potential prey, and determination of digestion rates.

Lastly, as the pelagic ocean is increasingly affected by anthropogenic pressures, addressing questions about food-web responses to specific disturbances requires baseline data on community composition and trophic interactions. Few studies (e.g., Robison et al. 1998; Silguero and Robison 2020; Briseño-Avena et al. 2020) have examined siphonophore abundances in relation to environmental variables. The effects of warming ocean temperatures, pollution, and increased fishing pressure on GZ abundances are debated (Condon et al. 2012), and it is unclear whether siphonophores are expected to change in abundance. Large-scale ocean deoxygenation may influence siphonophore abundance as gelatinous predators are generally tolerant of hypoxia (Mackie and Mills 1983; Thuesen and Childress 1994; Purcell and Arai 2001). As the populations of animals with lower hypoxia tolerances such as fishes and cephalopods decrease, siphonophores could fill those vacant food-web niches. Studies that examine both siphonophore abundances and diets across environmental gradients can provide insight into how their trophic interactions may impact food web dynamics under differ oceanographic conditions. The results from this review highlight the importance of siphonophores as mid-trophic predators and prey in the midwater food web and identify the most pressing knowledge gaps on the trophic role of these elusive yet ubiquitous animals.

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