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REVIEW

A review of benthic cnidarians as underappreciated predators in the gelatinous ocean

Ramón D. Morejón-Arrojo[1] · Florian Lüskow[2,3] · Evgeny A. Pakhomov[2,3] · Sergio D. Guendulain-García[4] · Wesley Dáttilo[5] · Leandro Rodríguez-Viera[6] · Bert W. Hoeksema[7,8]

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Abstract
Elucidating predatory interactions between benthic cnidarians (represented by scleractinian corals and sea anemones) and gelatinous zooplankton (GZ) is fundamental for understanding energy transfer pathways linking pelagic and benthic marine ecosystems. Based on published predation records, we constructed a bipartite predator-prey network comprising 44 benthic cnidarian species and 21 GZ taxa (cnidarians, ctenophores, thaliaceans). The network exhibited low connectance (7.2%) and a non-nested and modular pattern species interactions. This suggests that more specialised predators tend to interact with specific subsets of gelatinous prey, likely because they reject certain prey items that do not meet their feeding requirements or because they were not available in their environment. Moreover, our findings showed that there are no strong dominant groups of benthic cnidarian species specialising in the consumption of GZ. Benthic cnidarians showed a robustness network value of 0.63, similar to the robustness network value of 0.52 for their GZ prey. It appears that both groups have similar ability to withstand species loss without significantly affecting the overall ecosystem function.Thaliaceans, especially salps and pyrosomes, emerged as key energetic prey, being consumed by 15 cnidarian species, likely due to their relatively high energy content. Interestingly, temperate regions tended to have more documented predation cases compared to the tropics, potentially driven by more opportunistic feeding under seasonally varying, prey-limited, conditions. While current bentho-pelagic coupling via gelatinous predation appears relatively specialised across this bipartite network, anticipated climate impacts disrupting plankton phenology and abundances may substantially modify this behaviour in the future. Quantifying GZ assimilation efficiencies and optimal prey sizes across benthic cnidarian taxa is crucial for fully comprehending the ecosystem implications of such bentho-pelagic couplings amid global change.

Keywords Bentho-pelagic coupling · Corals · Food web · Gelatinous plankton · Nutrient and energy flux · Sea anemones

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Introduction

Gelatinous zooplankton (GZ) are a diverse group of marine organisms, including cnidarians, ctenophores, and thaliaceans (doliolids, pyrosomes, and salps), characterised by their soft, compliant, body, near-translucency, high body water content, and lack of exoskeletons (Madin and Harbison 2001; Jaspers et al. 2015). While GZ were traditionally considered of little energetic importance (and nutritional value) to higher trophic predators, recent studies showed that this is not always the case (Stenvers et al. 2020; Lüskow et al. 2021, 2022). Ranging in size from sub-millimetre to several meters, GZ exert substantial influence on marine ecosystems, particularly through predator-prey interactions, biogeochemistry and trophic dynamics (Cardona et al. 2012; Henschke et al. 2016; Hays et al. 2018; Thiebot and McInnes 2020; Chi et al. 2021). In this sense, they are shown to affect phyto- and zooplankton stocks and fish populations due to their high consumption rates and direct competition and predation on early fish life cycle stages (Jaspers et al. 2015; Brodeur et al. 2021; Heneghan et al. 2023). Despite their ecological relevance, GZ often receive little attention in zooplankton surveys (Wright et al. 2021).

Benthic cnidarians, including sea anemones (Actiniaria) and corals (especially Scleractinia), constitute vital components of coastal and reef ecosystems, contributing to habitat complexity and diversity. As ecosystem engineers, stony corals provide a three-dimensional structural complexity that promotes high levels of biomass and biodiversity by creating nurseries and shelters for countless species of fish and invertebrates (Montano 2022; van der Schoot and Hoeksema 2022, 2024; Guendulain-García et al. 2024). Moreover, coral reefs have tremendous ecological and economic value – protecting coastlines from storms and erosion, forming sandy beaches, supporting fisheries, attracting tourists (Lee et al. 2019; Fezzi et al. 2023).

In shallow, tropical waters, coral metabolism relies primarily on the symbiotic relationship with photosynthetic algae of the family Symbiodiniaceae (LaJeunesse et al. 2018). Through photosynthesis, they can provide up to 90% of the host's metabolic requirements (Trench 1979; Lesser 2007). This relationship allows corals to grow and create reefs in tropical oligotrophic waters (Berkelmans and van Oppen 2006). While such zooxanthellate corals are known to consume zooplankton, this nutritional source is commonly considered of secondary importance (Houlbrèque and Ferrier-Pagès 2009). However, heterotrophic feeding is critical for nutrient acquisition, particularly nitrogen, under normal physiological conditions (Grottoli et al. 2006). Besides obtaining energy via photosynthesis, scleractinian corals supplement their diets via (1) predation on pelagic and benthic animals (Palardy et al. 2005), which can be of relatively large size (Mehrotra et al. 2015, 2019; ter Horst and Hoeksema 2021; Gregorin et al. 2022), or small, such as bivalve molluscs, pteropod gastropods, ascidians, and annelid worms (Goldberg 2018; Lindemann et al. 2019), and (2) assimilation of dissolved organic and inorganic compounds (Houlbrèque and Ferrier-Pagès 2009). In addition to small prey items, benthic cnidarians are known to consume larger prey (macro-predation), including, larger ctenophores and jellyfish (Ates 2017; Gregorin et al. 2024a). The size ratio between prey and predator typically does not exceed 20 to 1, with prey often being equal to or up to 10 times larger than the polyp's oral disc. Size metrics are often inconsistently reported, as some studies measure at the basal disc rather than the oral disc (Acuña and Zomponi 1996). Various species engage in large-prey predation, with average prey-to-predator size ratios of 1:4.6 for solitary polyps and 1:11.8 for colonial forms (Gregorin et al. 2024a).

Cold-water corals, globally distributed in deep oceanic waters and shallow temperate latitudes, lack zooxanthellae and are entirely heterotrophic, but their zooplanktonic prey species are usually not taxonomically identified (Roberts et al. 2006; Maier et al. 2023). Classic experimental feeding studies have been more focussed on feeding mechanisms than on the natural prey choice (Carpenter 1910; Vaughan 1912; Boschma 1925; Yonge 1930; Abe 1938). However, recent research on natural prey selection and food processing in corals has started to gain popularity. For instance, van Oevelen et al. (2016) conducted a laboratory experiment on food selectivity by the cold-water coral *Lophelia pertusa* (accepted as *Desmophyllum pertusum* (Linnaeus, 1758)), highlighting the importance of prey choices in coral nutrition. Additionally, studies by Purser et al. (2010) and Mueller et al. (2013) provided additional insights into the feeding strategies and dietary preferences of various coral species, emphasising the need to consider both feeding mechanisms and prey selection in understanding the trophic ecology of corals. Macrophagous predation by scleractinians in situ is poorly studied, but is receiving growing attention (Gregorin et al. 2024a).

As another group of anthozoans, actiniarians (sea anemones) also play major roles as benthic food web components, but predominantly in temperate to polar regions in intertidal to deep-sea environments (Andrade et al. 2016; Sun et al. 2022). They are known for their predatory behaviour, capturing, and retaining planktonic (ranging from phytoplankton to fishes) and benthic prey of various sizes (Fautin and Fitt 1991; Acuña and Zomponi 1996; Jarms and Tiemann 2004; Quesada et al. 2014; Hoeksema et al. 2015; Ates 2017; Sun et al. 2022). Certain species, e.g. *Actinostola callosa* (Verrill, 1882), *Actinauge cristata* Riemann-Zürneck, 1986, and *Urticina* sp. Ehrenberg, 1834, are considered opportunistic polyphagous carnivores that can feed on relatively large planktonic prey items (Sun et al. 2022) constituting prime examples of bentho-pelagic coupling.

The interactions between benthic cnidarians and GZ, particularly the predatory behaviour of the former towards the latter, are of particular interest for understanding the dynamics of shallow coastal and deep oceanic ecosystems, which could have significant implications for marine food web structure and stability (Arai 2005). Along spatial and temporal gradients, various species of benthic cnidarians and GZ interact, forming complex networks of ecological, often mutualistic, interactions (Robinson et al. 2013; Dáttilo and Rico-Gray 2018). The earliest records of cnidarian predation on large plankton (including GZ) were perhaps made by Vaughan (1912), who reported that species of Caribbean reef coral can predate upon jellyfish, *Linuche* sp., salps, *Salpa "domestica"* (nomen nudum), and chaetognaths, *Sagitta* sp.

In recent decades, there have been local increases in the frequency and intensity of GZ blooms with significant implications for benthic communities (Lebrato et al. 2022). Following these blooms, sinking GZ carcasses transport labile carbon (and other nutrients) to benthic continental margins and the deep sea impacting biogeochemical and ecological water column processes (Orlov and Pakhomov 2024). GZ enhance carbon fluxes via both dissolved organic and inorganic carbon (Lebrato et al. 2019) underscoring the GZ ecological significance in global carbon cycling and marine ecosystem functioning (Luo et al. 2020, 2022).

Understanding the complex interactions between benthic cnidarians and GZ is crucial, as changes in the abundance and distribution of GZ could significantly alter the energetic and nutrient linkages between pelagic and benthic realms. Factors like eutrophication, overfishing, and climate change have been driving shifts in GZ populations (Luo et al. 2020, 2022).

Quantifying the predatory interactions between benthic cnidarians and different GZ taxa, as well as understanding their nutritional value and assimilation efficiency, will help elucidate the ecosystem-level implications of bentho-pelagic coupling under different global change scenarios. Moreover, additional comparative research is essential to comprehend how gelatinous predation rates might differ across various latitudes and anthozoan species, considering the limitations posed by oligotrophic *versus* prey-replete conditions (Hays et al. 2018). Such research will be crucial for predicting the future structure and functioning of marine ecosystems in the face of ongoing environmental changes.

The present study explores the ecological network of feeding interactions between benthic cnidarians as predators (corals: Scleractinia and pennatuloidean octocorals; sea anemones: Actiniaria; Ceriantharia) and GZ as prey, including cnidarian jellyfish, ctenophores, and thaliaceans: doliolids, pyrosomes, and salps. We reviewed the current state of knowledge on predation reports indicative of bentho-pelagic coupling, identified gaps and suggested directions for future research. We hypothesise that (H_1) benthic cnidarians are more likely to prey on thaliaceans (doliolids, pyrosomes, and salps) and ctenophores than jellyfish because (a) they lack nematocysts, which pose potential harm to the consumer, and (b) the energetic content of thaliaceans is higher than that of jellyfish. We further hypothesise that (H_2) predatory interactions are more likely to be opportunistic in temperate regions compared to tropics due to seasonality in the food supply.

Materials and methods

Data mining

A systematic review was conducted to evaluate the role of benthic cnidarians as underappreciated predators in the gelatinous ocean ecosystem. A comprehensive literature search was performed across multiple databases, including Google Schoolar, Scopus, and Web of Science, using a predefined set of keywords. The search queries utilised specific combinations of terms such as "salpivory", "benthic cnidarian", "predation", "prey", "gelatinous zooplankton", "jellyfish", "coral", and "sea anemone", employing Boolean operators (AND, OR) to refine the results. The literature search comprises publications from the year 1912 to 2025 to capture recent studies relevant to this topic.

Eligibility criteria were established to ensure the inclusion of high-quality studies: only peer-reviewed articles that focussed explicitly on the predatory behaviour of benthic cnidarians were considered. Studies that were opinion pieces, or did not provide primary data were excluded. The screening process involved the titles and abstracts of all identified records. Full texts of the articles that met the initial criteria were subsequently reviewed to confirm eligibility. We only take into account for this research species to species interactions, including genus records from both predator and prey taxa. References within the articles were also reviewed.

We then generated an adjacency matrix between benthic cnidarians as predators (scleractinians and actiniarians plus ceriantharians) and GZ: cnidarians, ctenophores, and thaliaceans. The matrix was based on the presence/absence of predation by benthic cnidarian species on GZ species. The current taxonomy of all species was corroborated using WoRMS (Worms Editorial Board 2024).

Data processing

Interaction network

The network of trophic interactions between benthic cnidarian species and GZ was constructed from the presence/absence data of predation between species. This interaction matrix was used to generate a bipartite graph, following the methodology suggested by Dormann et al. (2009). In such a bipartite graph, nodes are divided into two disjoint sets: the left set represents benthic cnidarian species, and the right set represents GZ species. Both categories, benthic cnidarian predators and GZ prey species, were divided in colour-coded taxonomic groups. Graph links (edges) connect species between levels and indicate predator-prey relationships.

Network descriptors

To characterise the network topology, five commonly used metrics were calculated: connectance and nestedness (NODF metric; Blüthgen et al. 2006; Guimarães et al. 2006), as well as modularity (Barber 2007), robustness, and vulnerability/generality (Bersier et al. 2002). Connectance quantifies the proportion of realised predator-prey interactions out of all possible interactions between benthic cnidarians and GZ. Higher connectance indicates greater trophic linkage between the predator and prey groups. Nestedness measures the hierarchical organisation of feeding interactions, specifically how the prey choices of specialist predators relate to those of generalist predators. In a nested network, specialist benthic cnidarians (those feeding on few gelatinous species) tend to prey upon a subset of the GZ species that are also consumed by more generalist cnidarians (those feeding on many species). High nestedness indicates that specialist predators are not choosing unique prey species, but rather are selecting from the same pool of prey species targeted by generalist predators, creating a hierarchical pattern in the food web structure. Modularity (Q) quantifies the degree to which benthic cnidarian and GZ species cluster into distinct modules with richer connectivity inside than between modules. A modular network indicates the groups that form distinct subgroups with limited interactions between modules. Robustness is the ability of a network to avoid co-extinctions after species loss, assessing the stability of the network if species are randomly removed, and focussing on functional redundancy as a buffer against secondary extinction cascades. Greater redundancy in trophic roles confers higher robustness to the food web overall. Vulnerability examines the average dependence of GZ prey species on their benthic cnidarian consumers. High vulnerability signifies high resource dependence on a few predator species. Generality measures the average number of gelatinous prey species exploited by benthic cnidarian predators. High generality indicates more diverse diets and low prey specificity; high = high dependence on few resources; low = low dependence on many resources. Generality measures the average number of resources exploited by species at a given trophic level; high = diverse diet; low = specialised diet (Bersier et al. 2002). All network metrics were determined using the plotweb function of the bipartite package (Dormann et al. 2009).

We tested the significance of nestedness and modularity for each network through null model analysis. For each metric, 1000 simulated random networks were generated using a null model that creates randomised bipartite networks, while preserving the original number of species, interactions, links, and connectance (Dormann et al. 2009). In this null model, the probability of an interaction occurring is proportional to the number of interactions of both benthic cnidarians and GZ. The observed nestedness and modularity values were then compared to the distribution of values from the 1000 null networks, allowing assessment of whether the observed metric values deviated significantly from what would be expected by chance for a network of equal size and species interaction frequencies. To test for differences in the predatory interactions between the tropical *versus* temperate zone, a Poisson log-linear regression model was fitted to the predation case data with location type (tropical *versus* temperate) as an independent variable. The tropical zone extends between the Tropic of Cancer (23°27′N) and the Tropic of Capricorn (23°27′S). The temperate zone is located from the Tropic of Cancer to the Arctic Circle (66°33′N) in the northern hemisphere and from the Tropic of Capricorn to the Antarctic Circle (66°33′S) in the southern hemisphere (Peel et al. 2007). The significance of the location-type regression coefficient was used to evaluate evidence for a difference in the predatory interactions between zones.

Finally, a map was plotted to visualise the global distribution of predation events of benthic cnidarian species on GZ species (cnidarians (hydro- and scyphomedusae), ctenophores, and thaliaceans) were recorded using the Geographic Information System software QGIS 3.28 (QGIS Development Team 2022). For all network analyses, we used R software and bipartite software (Dormann et al. 2009; R Core Team 2023) version 4.3.1.

Results

Network description

Our systematic review, covering publications from 1912 to February 2025, identified 36 unique publications containing relevant predation events involving benthic cnidarians and gelatinous zooplankton (GZ). We conducted searches across Google Scholar, Scopus, and Web of Science using eight specific search term combinations, which initially yielded 53,898 results. After applying rigorous exclusion criteria, we retained 36 publications, with a 65% overlap between databases. Additionally, we included 12 relevant sources cited in these papers, but not captured in our initial searches. The final count of relevant articles is detailed in a supplementary table (Table S1), which summarises the number of outcomes per search, the actual number of useful articles found, and the excluded documents for each query term across the three databases. This table enhances the transparency and reproducibility of our review methodology and provides a clear overview of the scope of literature consulted. The generated network is composed of 42 predator taxa of Cnidaria (class Hexacorallia: orders Actiniaria, Antipatharia, Ceriantharia, Scleractinia, and Zoantharia; class Octocorallia: order Scleralcyonacea (family Corallidae, superfamily Pennatuloidea) interacting as predators with 21 prey taxa (17 cnidarians, 1 ctenophore, and 3 thaliaceans) of GZ as prey. Sea anemones are represented by 17 taxa, while corals have 25 taxa (Table 1). Of the total number of possible predator-prey associations (924), 45 associations were recorded, equivalent to a connectance of 7.2% (Fig. 1). The taxa with the highest number of associations were the temperate anemone *Urticina felina* (Linnaeus, 1761) (5 prey), the temperate anemone *Metridium senile* (Linnaeus, 1761) (4 prey), the deep-sea actiniarian *Cylista troglodytes* (Price in Johnston, 1847) (4 prey), and the shallow-water sea anemone *Actinia equina* (Linnaeus, 1758) (3 prey; Fig. 1). All predation observations recorded in this study pertain to live GZ, specifically cnidarians, ctenophores, and thaliaceans. We acknowledge that while dead gelatinous plankton can contribute to nutrient cycling when they sink to the seabed, this study focusses exclusively on interactions involving live prey.

The most preyed upon organisms were salps (Salpidae sp.; 15 predators), the common jellyfish *Aurelia* spp. (Lamarck, 1816) (10 predators), the scyphozoan jellyfish *Pelagia noctiluca* (Forsskål, 1775) (8 predators), and scyphozoan jellyfish *Chrysaora hysoscella* (Linnaeus, 1767) (4 predators; Fig. 1). Within the marine food web, salps and pyrosomes are types of GZ that are important prey items for many species. Specifically, data show that salps constitute the prey of 14 different coral and sea anemone species that feed on GZ. This highlights the key trophic link that these thaliaceans provide between primary production and benthic cnidarian predators (Fig. 1), and also validates our first hypothesis (H_1), suggesting that benthic cnidarians are more likely to prey on thaliaceans and ctenophores than other GZ. However, ctenophores are only represented by a single prey species preyed on by two temperate-water actiniarians (Table 1).

The null models show that our network displays non-nestedness ($NODF = 7.01$, $p > 0.05$) and a modular ($M = 0.68$; $p < 0.01$) pattern of species interactions. The predators showed a slighty similar robustness ($R = 0.63$) compared to the GZ (cnidarians, ctenophores, and thaliaceans) prey ($R = 0.52$) within the network. This suggests similar functional redundancy in both trophic levels. The average generality (i.e., number of resource species per consumer) was 7.1, whereas the average vulnerability (i.e., number of consumer species per resource) was 2.1. This further suggests predators tended to consume a moderate number of prey on average, while prey taxa appeared to have a more specialised relationship with their predators, indicating that they are consumed by fewer predator species compared to the more generalist benthic cnidarians specialised, with only ~ two predator species each.

The predation network between benthic cnidarians and GZ organisms revealed a well-defined modular structure, with a total of 9 distinct modules identified (Fig. 2). These modules represent groups of species that interact more closely with each other than with species from other modules. This modular organisation suggests potential patterns of specialisation in the predator-prey interactions, where certain benthic cnidarians may be preying upon specific groups of GZ to a greater extent.

Latitudinal comparison of predator-prey association numbers

Predation cases were more common in the temperate zones (16 studies), compared to the tropical ones (11 studies; Fig. 3). However, the Poisson regression model showed that location type (temperate *versus* tropical) was not a significant predictor of the predatory interactions between benthic cnidarians and GZ taxa ($p = 0.59$). The tropical location type coefficient was 0.12, indicating an estimated 13.8% higher mean predatory interactions compared to temperate locations (on the logarithmic scale). However, substantial uncertainty existed around this estimate ($SE = 0.24$). Therefore, H_2 (expecting that predatory interactions are more likely to be opportunistic in temperate regions compared to tropics due to seasonality in the food supply) is rejected, although there are differences in the frequency of predation records between the tropical and temperate zones, which will be discussed below.

Table 1 List of reports of benthic cnidarian predators (corals and sea anemones) and their prey species of the gelatinous zooplankton (cnidarians (classes Hydrozoa and Scyphozoa), ctenophores (class Tentaculata), and thaliaceans)

Cnidarian (anthozoan) predator	Gelatinous zooplankton class	Gelatinous zooplankton prey	Location(s)	Reference
Hexacorallia: Actiniaria				
Actinia equina (Linnaeus, 1758)	Tentaculata	*Pleurobrachia pileus* (O. F. Müller, 1776)	North Sea	Den Hartog (1963)
Actinia equina (Linnaeus, 1758)	Scyphozoa	*Cyanea lamarckii* Péron & Lesueur, 1810	Channel Islands, England	Wood (2013)
Actinoscyphia aurelia (Stephenson, 1918)	Thaliacea	Pyrosomatidae sp. Lahille, 1888	Ivory Coast	Lebrato and Jones (2009)
Actinostola callosa (Verrill, 1882)	Scyphozoa	*Periphylla periphylla* (Péron & Lesueur, 1810)	Norwegian waters	Jarms and Tiemann (2004)
Anthopleura elegantissima (Brandt, 1835)	Hydrozoa	*Velella velella* (Linnaeus, 1758)	Northeastern Pacific	Francis (1973), Wertheim (1984)
Diadumene cincta Stephenson, 1925	Hydrozoa	*Eutonina indicans* (Romanes, 1876)	Oosterschelde, Netherlands	Ates (2017)
Diadumene leucolena (Verrill, 1866)	Scyphozoa	*Chrysaora quinquecirrha* (Desor, 1848)	Western Atlantic	Cones and Haven (1969)
Metridium farcimen (Brandt, 1835)	Scyphozoa	*Cyanea capillata* (Linnaeus, 1758)	Northeastern Pacific	Ates (2017)
Metridium senile (Linnaeus, 1761)	Hydrozoa	*Aequorea victoria* (Murbach & Shearer, 1902)	Northeastern Pacific	Ates (2017)
Metridium senile (Linnaeus, 1761)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Grevelingen, Netherlands	Ates (2017)
Metridium senile (Linnaeus, 1761)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Oosterschelde, Netherlands	Ates (2002)
Metridium senile (Linnaeus, 1761)	Tentaculata	*Pleurobrachia pileus* (O. F. Müller, 1776)	Oosterschelde, Netherlands	Greve (1972), reviewed in Ates (2002)
Metridium senile (Linnaeus, 1761)	Scyphozoa	*Chrysaora hysoscella* (Linnaeus, 1767)	Oosterschelde, Netherlands	Ates (2002)
Cylista elegans (Dalyell, 1848)	Scyphozoa	*Chrysaora hysoscella* (Linnaeus, 1767)	Oosterschelde, Netherlands	Ates (2017)
Cylista troglodytes (Price in Johnston, 1847)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Oosterschelde, Netherlands	Ates (2002)
Cylista troglodytes (Price in Johnston, 1847)	Scyphozoa	*Cyanea lamarckii* Péron & Lesueur, 1810	Oosterschelde, Netherlands	Ates (2002)
Cylista troglodytes (Price in Johnston, 1847)	Scyphozoa	*Chrysaora hysoscella* (Linnaeus, 1767)	Oosterschelde, Netherlands	Ates (2002)
Cylista troglodytes (Price in Johnston, 1847)	Hydrozoa	*Eutonina indicans* (Romanes, 1876)	Oosterschelde, Netherlands	Ates (2014)
Entacmaea medusivora Fautin and Fitt 1991	Scyphozoa	*Mastigias papua* (Lesson, 1830)	Lake Kakaban, Indonesia; Palau	Fautin and Fitt (1991), Hoeksema et al. (2015)
Entacmaea medusivora Fautin and Fitt 1991	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Lake Kakaban, Indonesia	Hoeksema et al. (2015)
Entacmaea medusivora Fautin and Fitt 1991	Scyphozoa	*Cassiopea ornata* Haeckel, 1880	Lake Kakaban, Indonesia	Hoeksema et al. (2015)
Urticina felina (Linnaeus, 1761)	Scyphozoa	*Rhizostoma pulmo* (Macri, 1778)	North Sea	Den Hartog (1963)
Urticina felina (Linnaeus, 1761)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Scotland	Wood (2005)
Urticina felina (Linnaeus, 1761)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Oosterschelde, Netherlands	Ates (2002)
Urticina felina (Linnaeus, 1761)	Scyphozoa	*Cyanea lamarckii* Péron & Lesueur, 1810	Oosterschelde, Netherlands	Ates (2002)
Urticina felina (Linnaeus, 1761)	Scyphozoa	*Chrysaora hysoscella* (Linnaeus, 1767)	Oosterschelde, Netherlands	Ates (2002)
Urticina felina (Linnaeus, 1761)	Scyphozoa	*Chrysaora hysoscella* (Linnaeus, 1767)	North Sea	Jarms and Tiemann (2004)
Urticina felina (Linnaeus, 1761)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Southwestern Ireland	Ates (2017)
Urticina eques (Gosse, 1858)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Unknown	Ates (2017)

Table 1 (continued)

Cnidarian (anthozoan) predator	Gelatinous zooplankton class	Gelatinous zooplankton prey	Location(s)	Reference
Urticina eques (Gosse, 1858)	Scyphozoa	*Phacellophora camtschatica* Brandt, 1835	Unknown	Ates (2017)
Urticinopsis antarctica (Verrill, 1922)	Scyphozoa	*Desmonema* sp. L. Agassiz, 1862	Southern Ocean	Conniff (2000)
Anemonia sulcata (Pennant, 1777)	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	Mediterranean Sea	Cerrano et al. (2016); Canovas and Gonzalez-Wanguemert (2018)
Anemonia sulcata (Pennant, 1777)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Mediterranean Sea	Cerrano et al. (2016)
Anemonia sulcata (Pennant, 1777)	Scyphozoa	*Rhizostoma pulmoi* (Macri, 1778)	Mediterranean Sea	Cerrano et al. (2016)
Anemonia viridis (Forsskål, 1775)	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	India	Padate et al. (2020)
Condylactis gigantea (Weinland, 1860)	Scyphozoa	*Cassiopea* sp. Péron & Lesueur, 1810	Florida Keys, Western Atlantic	Morejón-Arrojo et al. (2025)
Condylactis gigantea (Weinland, 1860)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Cuba, Caribbean Sea	Morejón-Arrojo et al. (2025)
Hexacorallia: Antipatharia				
Antipathella subpinnata (Ellis & Solander, 1786)	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	Mediterranean Sea	Cerrano et al. (2016)
Hexacorallia: Ceriantharia				
Ceriantheopsis americana (Agassiz in Verrill, 1864)	Thaliacea	Pyrosomatidae sp. Lahille, 1888	Ivory Coast	Lebrato and Jones (2009)
Synarachnactis lloydii (Gosse, 1859)	Hydrozoa	*Neoturris pileata* (Forsskål, 1775)	Scotland	Ates (2017)
Hexacorallia: Scleractinia				
Astroides calycularis (Pallas, 1766)	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	Mediterranean Sea	Musco et al. (2018)
Cycloseris costulata (Ortmann, 1889)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Cycloseris fragilis (Alcock, 1893)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Danafungia scruposa (Klunzinger, 1879)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Danafungia scruposa (Klunzinger, 1879)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Red Sea	Alamaru et al. (2009)
Dendrogyra cylindrus (Ehrenberg, 1834)	Scyphozoa	*Linuche* sp. Eschscholtz, 1829	Bahamas, Caribbean Sea	Vaughan (1912)
Fungia fungites (Linnaeus, 1758)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Halomitra pileus (Linnaeus, 1758)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Heliofungia actiniformis (Quoy & Gaimard, 1833)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Herpolitha limax (Esper, 1792)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Heteropsammia cochlea (Spengler, 1781)	Thaliacea	*Iasis* cf. *cylindrica* (Cuvier, 1804)	Gulf of Thailand	Mehrotra et al. (2016)
Heteropsammia cochlea (Spengler, 1781)	Thaliacea	Salpidae sp. Lahille, 1888	Gulf of Thailand	Mehrotra et al. (2023)
Heteropsammia cochlea (Spengler, 1781)	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	Gulf of Thailand	Mehrotra et al. (2023)
Madracis auretenra Locke et al.2007	Thaliacea	Salpidae sp. Lahille, 1888	Curaçao, Caribbean Sea	ter Horst and Hoeksema (2021)
Manicina areolata (Linnaeus, 1758)	Thaliacea	*Salpa* sp. Forsskål, 1775	Bahamas, Caribbean Sea	Vaughan (1912)
Meandrina meandrites (Linnaeus, 1758)	Thaliacea	Salpidae sp. Lahille, 1888	Curaçao, Caribbean Sea	ter Horst and Hoeksema (2021)
Montastraea cavernosa (Linnaeus, 1767)	Thaliacea	Salpidae sp. Lahille, 1888	Curaçao, Caribbean Sea	ter Horst and Hoeksema (2021)
Pleuractis moluccensis (Van der Horst, 1919)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)

Table 1 (continued)

Cnidarian (anthozoan) predator	Gelatinous zooplankton class	Gelatinous zooplankton prey	Location(s)	Reference
Pleuractis paumotensis (Stutchbury, 1833)	Thaliacea	Salpidae sp. Lahille, 1888	Kota Kinabalu, Malaysia	Hoeksema and Waheed (2012)
Pseudodiploria clivosa (Ellis & Solander, 1786)	Scyphozoa	*Linuche* sp. Eschscholtz, 1829	Bahamas, Caribbean Sea	Vaughan (1912)
Siderastrea siderea (Ellis & Solander, 1786)	Scyphozoa	*Linuche* sp. Eschscholtz, 1829	Bahamas, Caribbean Sea	Vaughan (1912)
Tubastraea micranthus (Ehrenberg, 1834)	Hydrozoa	*Aequorea* sp. Péron & Lesueur, 1810	Suez Gulf, Red Sea	Gregorin et al. (2022)
Leptopsammia pruvoti Lacaze-Duthiers, 1897	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	Mediterranean Sea	Cerrano et al. (2016)
Leptopsammia pruvoti Lacaze-Duthiers, 1897	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Mediterranean Sea	Cerrano et al. (2016)
Leptopsammia pruvoti Lacaze-Duthiers, 1897	Scyphozoa	*Rhizostoma pulmo* (Macri, 1778)	Mediterranean Sea	Cerrano et al. (2016)
Hexacorallia: Zoantharia				
Parazoanthus axinellae (Schmidt, 1862)	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	Mediterranean Sea	Cerrano et al. (2016)
Parazoanthus axinellae (Schmidt, 1862)	Scyphozoa	*Aurelia* sp. Lamarck, 1816	Mediterranean Sea	Cerrano et al. (2016)
Parazoanthus axinellae (Schmidt, 1862)	Scyphozoa	*Rhizostoma pulmo* (Macri, 1778)	Mediterranean Sea	Cerrano et al. (2016)
Savalia savaglia (Bertoloni, 1819)	Scyphozoa	*Pelagia noctiluca* (Forsskål, 1775)	Mediterranean Sea	Cerrano et al. (2016)
Octocorallia: Scleralcyonacea				
Anthomastus bathyproctus Bayer, 1993	Thaliacea	Salpidae sp. Lahille, 1888	Antarctic, Gulf of Thailand	Gili et al. (2006)
Octocorallia: Pennatuloidea				
Pennatula sp. Linnaeus, 1758	Thaliacea	Pyrosomatidae sp. Lahille, 1888	Ivory Coast	Lebrato and Jones (2009)

Discussion

The analysis of the predation network revealed a non-nested pattern of resource use, indicating that interaction patterns do not conform to a nested structure. According to Krishna et al. (2008), a nested pattern arises when more abundant species of benthic cnidarians interact with each other, while rarer species tend to interact primarily with these abundant species, resulting in limited interactions between rare species. However, in the context of our findings, the absence of a nested structure indicates that interactions among species are more diverse and complex. The non-nested pattern suggests that specialised benthic cnidarians do not consistently interact with a specific subset of gelatinous prey. Instead, both potential abundant and rare species may engage with a broader range of prey types, leading to a more intricate network of interactions. This complexity reflects the ecological dynamics of the system, where interactions are not solely determined by relative abundance of benthic cnidarian species and GZ taxa, but also by other ecological and environmental factors. We found a modular pattern of species interactions, indicating that there are groups of species that connect more strongly among themselves than with other species in the network, forming distinct modules characterised by tighter connections within each module compared to interactions between different modules. This modular pattern could arise due to various ecological, environmental, or morphological filters that influence species interactions, such as habitat preferences, prey availability, or specific adaptations that facilitate or constrain certain interactions (Marquitti et al. 2014).

In the context of the predator-prey interactions between benthic cnidarians and GZ, modularity may stem from specific adaptations such as the feeding mechanisms of benthic cnidarians, which vary in structure and function, enabling them to capture different sizes and types of gelatinous prey. For example, certain corals may possess longer tentacles suited for capturing larger prey (Price and Patterson 2023), while sea anemones may exhibit more versatile feeding strategies that allow them to consume smaller zooplankton (Robinson et al. 2013). Additionally, environmental factors like water temperature, salinity, and nutrient availability can influence not only the amount, but the prey species present (Geertsma et al. 2022), determining the interaction patterns observed within the network. Furthermore, water flow plays a critical role in determining interaction patterns within the network, as it affects both tentacular crown size and capture efficiencies, which in turn influence variability in prey capture dynamics. Water flow influences the expansion and contraction of the tentacular crown, directly affecting the

Fig. 1 Predation network between benthic cnidarians (corals and sea anemones) and gelatinous zooplankton (GZ; cnidarians, ctenophores, and thaliaceans). Links between nodes indicate that a species in the first column preys on the species it is connected to. The size of the nodes (rectangles) is proportional to the number of predation/prey cases. The connectance value for the benthic cnidarian-GZ network was 0.072, indicating that 7.2% of possible links between species were realised

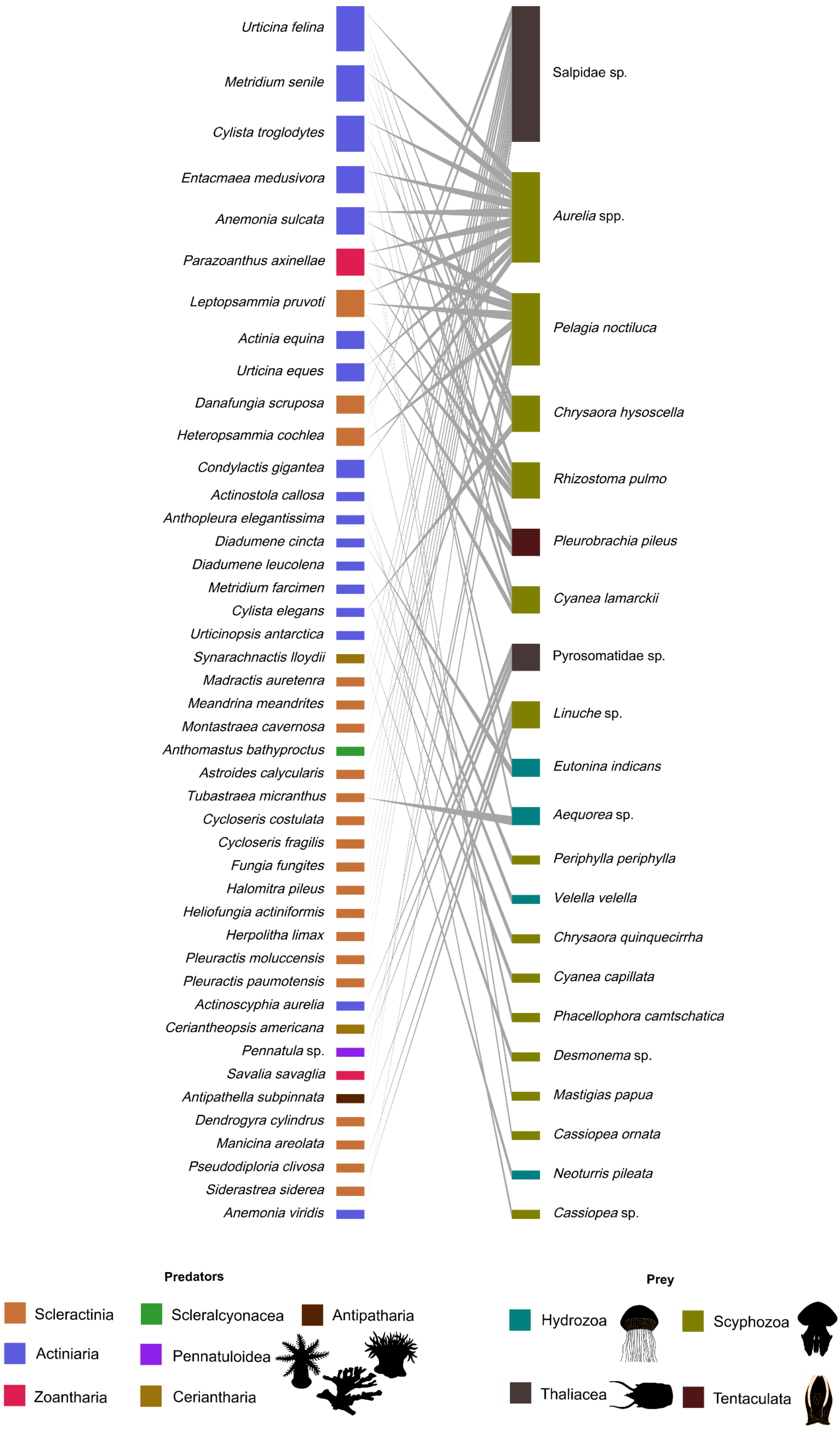
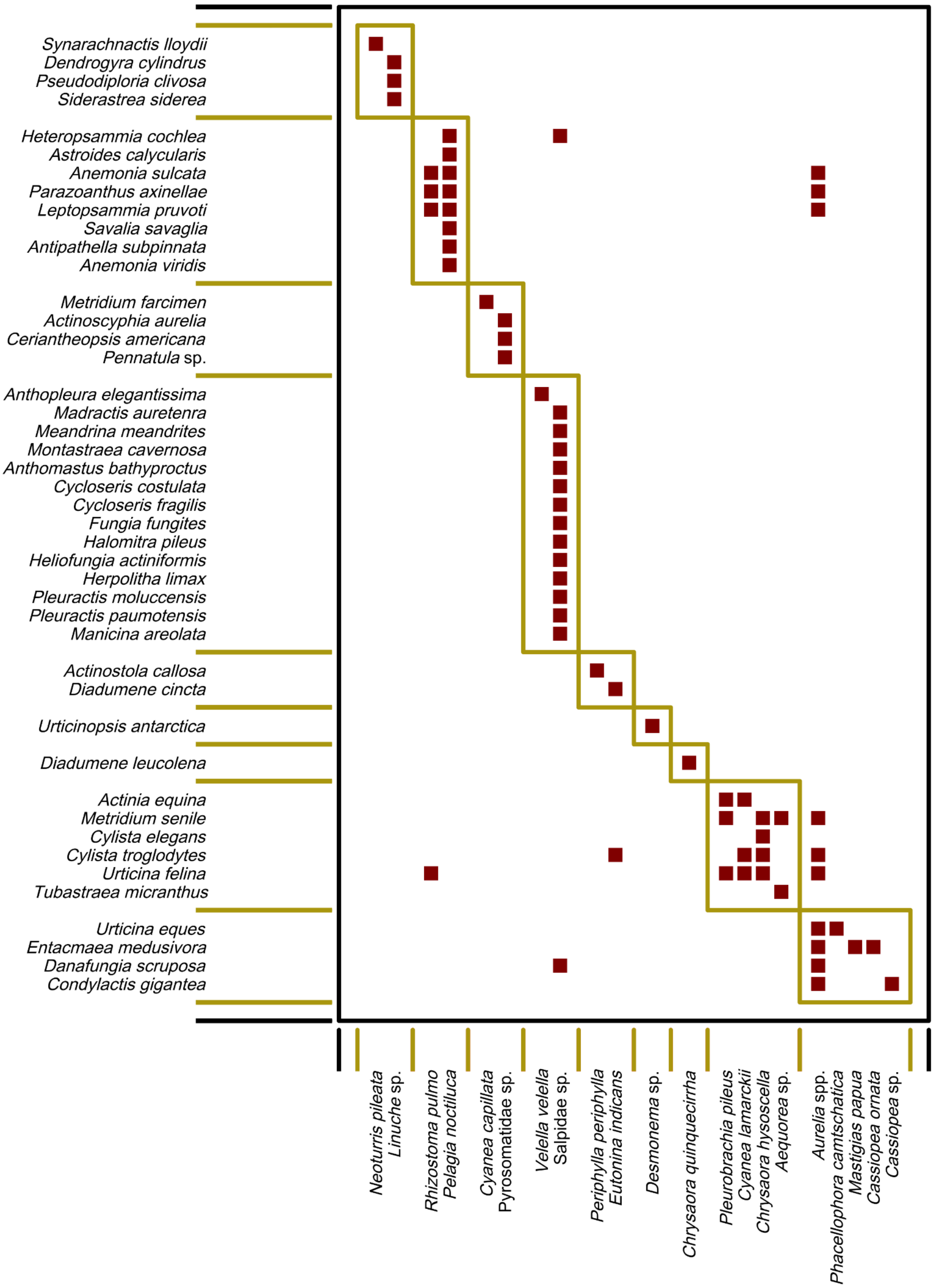


Fig. 2 Modules of the predation network of benthic cnidarians (corals and sea anemones) and gelatinous zooplankton (GZ; cnidarians, ctenophores, and thaliaceans). The y-axis represents predators and the x-axis represents prey



surface area available for prey capture. In moderate flow conditions, tentacles remain extended, increasing encounter rates with prey, whereas, in high-flow environments, polyps may retract their tentacles to prevent damage, reducing capture efficiency (Geertsma et al. 2022). Benthic cnidarians, such as scleractinian corals and sea anemones, exhibit a variety of feeding strategies, from suspension feeding to opportunistic predation, therefore, access to a diverse prey types (Sebens 1981). Similarly, GZ comprise a diverse assemblage of organisms with different sizes, shapes, and life history strategies (Haddock 2004). It is important to note that this study collected data at large spatial and temporal scales, which may have underlay more specific patterns that could have emerged at finer scales. Indeed, predator-prey interaction patterns may vary across space and time and are influenced by local environmental factors such as water temperature, salinity, nutrient availability, and the presence of physical structures like reefs or seagrass beds. These factors can affect the distribution and abundance of both benthic cnidarians and GZ, shaping their interaction patterns. Additionally, resource availability, life stages of

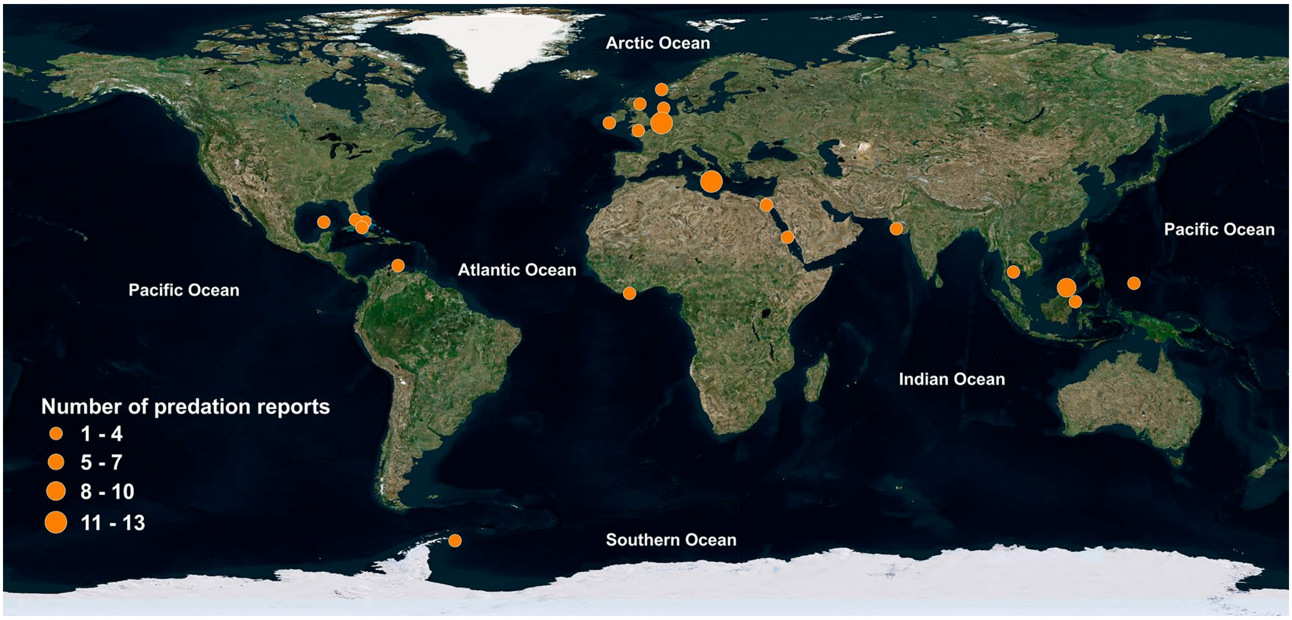


Fig. 3 Distribution of published predation records of corals and sea anemones on gelatinous zooplankton (cnidarians, ctenophores, and thaliaceans). Data are taken from Table 1

both predators and prey, and species-specific behaviours also play critical roles in these dynamics (Singh et al. 2021).

The average generality was 7.1 prey types per predator, classifying most as intermediate generalists (Bersier et al. 2002). GZ exhibited higher vulnerability, as each prey species was typically exploited by around two predator species. Simulated robustness was similar for predator corals and sea anemones than GZ prey, implying greater redundancy among the former (Bersier et al. 2002). This likely arises from similarities in opportunistic feeding modes within anthozoan subclasses (Chintiroglou and Koukouras 1992; Ivanova and Grebelnyi 2017). Overall, the average number of consumer species per resource was low (2.1 consumer species exploiting each GZ species), suggesting specialised interactions, were GZ are primarily targeted by a limited number of predator species. Hence, the removal of certain GZ species, would result in the loss of unique functional roles within the ecosystem, for example, predators relying on a particulare GZ pray, may face significant challenges in finding alternative food sources. Future studies should prioritise monitoring programmes that identify key predators consuming multiple prey including a highly exploited vulnerable prey (Arai 2005). Once identified, both the key predator species and vulnerable GZ prey species should be targeted for protection, as doing so would help confer stability to the overall ecosystem. Removal experiments, both in situ and in laboratory model systems, can be a valuable tools in elucidating the ecosystem impacts stemming from the loss of important taxa.

Gelatinous zooplankton as prey for benthic cnidarians

The relative, i.e., weight-specific, energy content of GZ taxa varies widely. While tentaculate ctenophores, such as *Pleurobrachia*, have a relatively low energy value of 3.8 ± 0.9 kJ g DW^{-1}, hydrozoans and scyphozoans are marginally energy-richer with 4.4 ± 2.4 and 5.4 ± 2.0 kJ g DW^{-1}, respectively. Thaliaceans, on the other hand, are significantly higher in energy content, with salps reaching 8.3 ± 3.4 kJ g DW^{-1}, while larvaceans (appendicularians) can have even higher energy contents (Lüskow et al. 2021). It is important to note that the energy content of GZ can also vary depending on their stomach contents, such as ingested copepods, which may further influence their nutritional value to predators (Hays et al. 2018; Lüskow et al. 2021). However, this source of variability was not explicitly accounted for in our study. A recent study by Lüskow et al. (2024) found that the residual water content, i.e., water remaining after drying, ranged from 1.5 to 20.6% of dry weight across seven pelagic tunicate species, with an average of 8.9 ± 4.2%. Furthermore, the total, i.e., weight-cumulative, individual energy content depends vastly on the size of the GZ specimen and can, in some cases, even surpass the total energy content of lipid-rich euphausiids and copepods (Lüskow et al. 2021; Fig. 10 therein). While in relative terms, euphausiids and copepods exceed GZ in energy content, their total energy content is most often lower than that of cnidarians, ctenophores, and thaliaceans (Lüskow et al. 2021; Jaspers et al. 2023). This may make GZ (cnidarians, ctenophores, and thaliaceans) attractive prey, although the energy costs associated with hunting larger individuals can vary and may be more costly than the energy content of the prey item, validating our first hypothesis (H_1), suggesting that benthic cnidarians are more likely to prey on thaliaceans and ctenophores than other GZ. This, however, assumes that the entire prey organism can be consumed by a predator. Considering the calyx sizes of corals and anemones, complete consumption of large prey like salps and jellyfish may not always be possible. Therefore, prey can only be partially consumed or alternatively entirely over long periods of time (Gregorin et al. 2024a). During the handling and ingestion of GZ, it is important to note that other potentially more energy-rich prey, such as euphausiids and copepods, can also be present in the environment. While the initial statement suggested that the simultaneous consumption of large and small prey is restricted, a study by Gregorin et al. (2024b) provides evidence that both prey types can co-occur and be co-consumed in natural settings, indicating that large prey may be considered an ephemeral food resource, while small prey is more consistently available. Therefore, cnidarians may exhibit flexible feeding strategies when multiple prey sources are available.

Digestion times also differ vastly among taxa, e.g., cnidarians are digested faster than ctenophores and chaetognaths (Martinussen and Båmstedt 2001). Whether it is more efficient for a benthic cnidarian to capture, ingest, digest, and assimilate one large GZ specimen in contrast to several smaller crustacean specimens remains to be determined. However, during GZ falls, large gelatinous plankton could readily be available for benthic cnidarians (Lebrato et al. 2012, 2019). Several examples from the reviewed data (Table 1) concern salps and jellyfish that occur in swarms and land down on shallow coral reefs, where they are consumed by corals (Alamaru et al. 2009; Hoeksema and Waheed 2012; Mehrotra et al. 2016; ter Horst and Hoeksema 2021). Therefore, it is plausible that consuming thaliaceans is energetically more rewarding than cnidarians and ctenophores, however, how they are digested by corals and sea anemones is currently unknown.

Additionally, while we have noted the dominance of certain GZ such salps and pyrosomes, our findings do not definitively demonstrate active selection of these prey items. The observed predation patterns may reflect the greater availability of these organisms in the environment reflecting rates of encounter, rather than a preference. Future research on predators feeding behaviours and selection processes is needed to fully indertand this predator-prey dynamics.

The relevance of prey size, shape and toxicity as prey selection criteria

Benthic cnidarians, including photosynthetic corals, have been described as consumers of large zooplankton (Palardy et al. 2005; Bos et al. 2011; Contreras-Vega et al. 2021). Due to their sessile condition, their main feeding strategy is opportunistic predation (Alamaru et al. 2009; Mehrotra et al. 2019). However, the size and morphological characteristics of benthic cnidarians (as individuals or as colonies) may determine the amount, size, and shape of the prey they can ingest (Waheed and Hoeksema 2012; Mehrotra et al. 2019). Large-mouthed (25–30 mm), but small free-living coral species such as *Heteropsammia cochlea* have been observed ingesting prey (40–50 mm long) larger than themselves, including salps and sea slugs (Mehrotra et al. 2016, 2019). A similar observation concerns the small medusivorous sea anemone *Entacmaea medusivora* Fautin and Fitt 1991, preying on three large jellyfish species in an Indonesian marine lake (Hoeksema et al. 2015). Moreover, large sacoglossan sea slug prey items (longer than 12 mm) were ingested rarel, and more slowly, compared to smaller individuals, indicating size limitations on ingestion capacity (Mehrotra et al. 2019).

Previous research has investigated prey capture in relation to tentacle crown and mouth size for some cnidarians, finding that larger species can capture more, and larger prey compared to smaller species (Sebens 1981; Acuña and Zamponi 1996). Furthermore, large and strong tentacles can capture and subdue larger prey, while small tentacles may only be able to handle small prey (Schlesinger et al. 2009; Morandini et al. 2016; Gregorin et al. 2024c). Species with large mouths, such as large mushroom corals and *H. cochlea*, can access a broad range of planktonic and benthic macrofauna compared to species with smaller mouths (Alamaru et al. 2009; Hoeksema and Waheed 2012; Mehrotra et al. 2016). While mouth size influences the ability to prey on large zooplankton like jellyfish, it is likely just one determining factor. Further research quantitatively examining the relationship between coral polyp size and dimensions of ingested prey would help elucidate these morphological constraints on heterotrophic feeding capacity. In addition, Sebens and Johnson (1991) demonstrated that coral species with different morphologies respond differently to variations in flow speed, affecting their ability to capture prey. For instance, species with long tentacles may experience reduced capture efficiency at higher flow speeds due to tentacle deformation, while branching corals may benefit from increased turbulence enhancing prey retention.

Additionally, the external shell of the sea slug *Aliculastrum debile* appeared to prevent its ingestion by a mushroom coral, while sea slugs without an external shell were readily consumed (Mehrotra et al. 2019). Although this example does not concern planktonic prey, it suggests that not only prey size, but the shape and structural integrity of prey items may affect whether they can be successfully ingested. Thus, the size and shape of a cnidarian polyp may have coevolved with the size range and shapes of available prey in its habitat.

Jellyfish contain toxins in their cnidae (Badré 2014; d'Ambra and Lauritano 2020), but it is unknown whether this may prevent some species from being ingested due to the rarity of documented observations of jellyfish captured by benthic cnidarians. There are examples of poisonous sea slugs being predated on by sea anemones in which it appears that the predators were not always successful (van der Meij and Reijnen 2012; Hayes and Schultz 2022). Therefore, it is possible that the venom of some jellyfish may protect them agains predation by benthic cnidarians.

Latitudinal comparison of predator-prey association numbers

Although the Poisson regression model did not show a statistically significant difference in predation records between zones, greater research effort and faunal familiarity in temperate areas could contribute towards more documented cases compared to the tropics. However, it is important to note that the number of studies was higher in temperate locations (16 studies since 1963) than in tropical locations (11 studies since 1912), which could have caused a geographical bias. On average, tropical marine zones tend to be more oligotrophic with lower nutrient availability compared to temperate areas like the highly productive North Atlantic and North Pacific (Field et al. 1998; Lønborg et al. 2021). In contrast to oligotrophic tropical areas, the consistently higher productivity in temperate oceans provides a more reliable food supply, potentially reducing reliance on opportunistic predation. While our findings indicate a higher frequency of predation events at high latitudes, we must consider that this pattern may be partially driven by a higher research activity in these areas. Future studies should aim to balance research efforts across latitudes to ensure a more comprehensive understanding of benthic cnidarian interactions with GZ. Further research quantifying predation rates concerning local productivity levels is still needed to fully evaluate the opportunistic feeding hypothesis. Targeted feeding studies have shown flexible opportunistic feeding behaviour by both temperate and tropical anthozoans (Boschma 1925; Chintiroglou and Koukouras 1992; Mehrotra et al. 2019), even involving artificial food (Ding et al. 2021). Overall, the need to supplement prey-limited periods in temperate zones may drive more frequent opportunistic jellyfish predation by benthic cnidarians facing seasonal limitations in their typical suspension-feeding diet. Understanding the constraints of oligotrophic conditions *versus* prey-replete periods on gelatinous predation rates merits more comparative investigation across latitudes and anthozoan species.

Bentho-pelagic coupling beyond cnidarians and ecosystem implications

While most studies have focussed specifically on cnidarian interactions, other gelatinous organisms like salps also contribute to link energy transfer between surface production and the benthos through other taxonomic groups. For example, gelatinous detritus is consumed by various echinoderms, molluscs, and crustaceans (Henschke et al. 2013). Sinking jelly-falls also subsidize deep-sea scavengers and microbiota when large surface blooms crash (Lebrato et al. 2019).

As climate change impacts plankton communities, bentho-pelagic couplings mediated by gelatinous groups may increase. This includes direct benthic predation, but also indirect nutrient linkage through microbial remineralisation and detrital pathways (West et al. 2009). Further research should adopt a whole-ecosystem perspective, integrating across different gelatinous-benthos connections, to elucidate current *versus* future carbon flow magnitudes. The predator-prey network suggests specialised feeding interactions between benthic cnidarians and GZ. However, the low connectance indicates these cross-system bentho-pelagic linkages are still limited – at least given the current state of knowledge. This implies that the transfer of energy and nutrients between the benthic and pelagic realms via gelatinous predator-prey interactions plays a relatively minor role compared to other pathways (see jelly web; Chi et al. 2021). However, with climate change and other anthropogenic stressors increasingly impacting both benthic and pelagic ecosystems (Lebrato et al. 2019), the ecosystem implications of such bentho-pelagic coupling warrant greater attention. For example, declining ocean oxygen levels could favour the expansion of hypoxia-tolerant gelatinous species, strengthening this pathway over time. Similarly, ocean acidification impacts could differentially affect the calcifying plankton that compete with GZ, again altering energy flows (McCormick and Levin 2017).

In coastal zones, increasing jellyfish and ctenophore abundance can have negative impacts like competition with juvenile fish (Brodeur et al. 2021). However, our results suggest limited reliance of tropical reef builders for GZ nutrition. Greater predation happens among temperate corals and anemones, possibly supplementing an otherwise nutrient-poor baseline diet (Coma et al. 1995). For deep-sea ecosystems, the vertical transport of gelatinous fallout can provide important short-lived, episodic and/or seasonal nutrition to benthic communities when large surface blooms of jellyfish, ctenophores or salps collapse (Lebrato et al. 2019, 2022). Gregorin et al. (2024a) synthesised reports of deep-sea cnidarians like anemones and corals consuming a variety of gelatinous organisms, suggesting this pathway plays an underappreciated role in transferring energy from pelagic to benthic realms, especially in food-limited deep habitats. While some temporal variability exists in gelatinous nutrient fluxes, climate change may alter the size, intensity, and phenology of pelagic gelatinous blooms (Luo et al. 2020, 2022). If the number of gelatinous carcasses falling down increases, active suspension feeders like sea anemones may benefit (Gili et al. 2006), but the consequences for passive suspension feeding corals and sponges are unknown. These findings related to clime change align with Gregorin et al. (2024c), who found that bleached *Exaiptasia diaphana* sea anemones exhibited reduced cooperative predation efforts on large jellyfish prey compared to unbleached conspecifics. This suggests symbiont loss impairs large prey capture capacities, highlighting how species-specific bleaching responses can impact GZ predation pathways.

Determining the tolerances of passive suspension feeders like some rals to episodic (often stochastic) gelatinous carcass deposition merits further study, as does quantifying potential recruitment or toxicity impacts on early coral life stages. While there has been considerable research on the effects of GZ carcass deposition on deep-sea benthic communities in areas like Norwegian fjords (e.g., Dunlop et al. 2017a, b; Sweetman et al. 2017), the dynamics likely differ substantially in shallow-water coral reef ecosystems. In shallow reef environments, GZ carcasses face greater predation pressure from pelagic fish (Bos et al. 2017; Morejón-Arrojo et al. 2024; Morejón-Arrojo and Rodríguez-Viera 2024), stronger physical disturbance from waves and currents, and faster decomposition rates due to higher temperatures and microbial activity (Orlov and Pakhomov 2024). These factors may limit the amount of GZ material reaching the reef benthos compared to deep-sea environments. Evaluations of GZ carcass deposition rates and their impacts on shallow-water coral reef communities are still lacking. Understanding these effects remains important given potential increases in jellyfish blooms in some regions due to possible factors like eutrophication, overfishing, and climate change (Mills 2001; Purcell et al. 2007; Bosch-Belmar et al. 2020; Clerc et al. 2023), although these factors are still considered uncertain and need to be tested (Fernández-Alías et al. 2024), while more attention need to be given to the biological role of life history traits (Boero et al. 2008). Additionally, does the nutritional value of gelatinous detritus differ between jellyfish, ctenophores, and thaliaceans (as well as appendicularians)? Are there species-specific effects for benthic communities beneath these pulses? By broadening the focus beyond just scyphozoan jellyfish to incorporate GZ more inclusively, we can better understand bentho-pelagic coupling via these sporadic organic matter subsidies under climate change (Tinta et al. 2023).

The nutritional value also depends on the gelatinous groups impacted. Our network suggests that benthic cnidarians have more opportunities to catch thaliaceans than scyphozoans, aligning with the higher energy content of the former compared to the latter (Lüskow et al. 2021) and often high carbon-to-phosphorus ratio (Lüskow et al. 2022), indicating different nutritional value. So, thaliacean increases could confer greater benthic benefits than proportionate jellyfish surges. However, understanding assimilation efficiencies and optimal prey sizes across different species is still required. Overall, bentho-pelagic couplings via predation on gelatinous fauna remain rather specialised. However, climate change impacts on both benthic species and seasonal plankton dynamics may alter energy flows and trophic dependencies in the future (Clerc et al. 2023). Quantitative data tracking rates of feeding on GZ taxa across anthozoan species instead of just occurrence data would better elucidate the ecosystem implications amidst global change.

Conclusions

This study provides the first comprehensive analysis of the predator-prey network linking benthic cnidarians and GZ, revealing relatively specialised and compartmentalised trophic linkages. However, thaliaceans like salps and pyrosomes, emerge as more common, energy-rich prey for diverse cnidarian predators, providing higher nutritional value compared to other gelatinous groups. Geographic patterns suggest more frequent predation on GZ in temperate *versus* tropical regions, tentatively implying opportunistic feeding compensates for seasonally prey-limited constraints at higher latitudes.

While contemporary bentho-pelagic coupling appears limited compared to previous jelly web network analyses, it represents an underexplored yet potentially critical energy pathway that could be profoundly altered by climate change impacts. Quantifying factors like prey preferences, assimilation efficiencies and ingestion rates across cnidarian taxa is crucial for forecasting how shifts in gelatinous prey availability may propagate through marine ecosystems. Resolving the mechanisms driving these predator-prey interactions between pelagic and benthic realms is imperative for holistically modelling ecosystem structure and functioning amid global change.

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Data availability Data are available on reasonal request.

Declarations

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