REVIEW PAPER

Big enough for an extra-large meal: a review on predation upon large animals by benthic cnidarians

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Abstract The feeding upon large animals—even larger than the predator—by benthic cnidarians has been reported from many ecosystems but never exhaustively studied to date. By reviewing 38 papers on this topic, this review aims to recap the observations on the predatory behaviour of polyps, to establish feeding plasticity boundaries and to understand the contribute of this trophic strategy to the benthic–pelagic coupling. The reviewed documents published increasingly during the last two decades mostly reported observations on heterotrophic Anthozoa in shallow ecosystems collected through photo/video records. The main prey items are represented by gelatinous zooplankton and echinoderms. The lexical discordance in the considered papers highlights the need to standardize the terminology to describe the feeding behaviour of benthic Cnidaria, opportunistic and characterized by a strong plasticity. Given the importance of large prey in cnidarian trophism, we proposed an unambiguous terminology that will help the online search of literature and address future studies. We suggest identifying micro-predation (predator/prey size ratio ≥ 5:1) and macro-predation (predator/prey size ratio is ≤ 1:1) as distinct feeding modalities, because the capture of large prey involves peculiar movements of polyps, such as stretching and retracting of column and tentacles to pull the prey towards the mouth.

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Introduction

Cnidarians are a major component of benthic communities worldwide (Spalding et al., 2001; Jarms & Tiemann, 2004; Shick, 2012; Burt et al., 2020;

Cummings et al., 2021; Sun et al., 2022; Grimes et al., 2023), inhabiting a multitude of environments highly variable in temperature, nutrients load and salinity, such as eutrophic coastal areas (Burt et al., 2020), anthropically disturbed areas (Soares et al., 2023), dark and deep ecosystems (Watling et al., 2011), hot hydrothermal vents (López González et al., 2003) and shallow tropical waters (Sheppard et al., 2017). Feeding modalities of benthic cnidarians include suspension-feeding of dissolved organic matter (amino acids, carbohydrates, urea), detrital (e.g. sediments) and live particulate organic matter (e.g. pico- and nanoplankton, prokaryotes and small eukaryotes such as ciliates) (Sieburth, 1978; Houlbrèque & Ferrier-Pagès, 2009), which allow the exploitation of nutrients carried by water currents (Diaz-Pulido & Garzón-Ferreira, 2002; Stuhldreier et al., 2015; Licer et al., 2023). Moreover, cnidarians are voracious predators of mesozooplankton (Sieburth et al., 1978; Gili et al., 2006; Houlbrèque & Ferrier-Pagès, 2009) constituted by holo-and meroplankton including eggs, juveniles and larvae of reef fauna, particularly abundant in specific daily intervals due to diel vertical migrations (Orejas et al., 2001; Gili et al., 2006). Mostly in oligotrophic shallow waters, some reef species display a symbiotic relationship with zooxanthellae, unicellular microalgae of the family Symbiodinaceae (LaJeunesse et al., 2018), which provide the cnidarian host with photosynthesized nutrients. The symbiotic exchange allows the coral host to fulfil up to 100% of their daily energetic demand (Muscatine et al., 1981; Grottoli et al., 2006). Analogously, mixotrophy characterizes sea anemones inhabiting the deep hydrothermal vents, which benefit from the mutualistic relationship with chemosynthetic bacteria (Goffredi et al., 2021). In addition to these variety of feeding modalities, several reports of capture and ingestion of macrofauna (e.g. echinoderms, medusae, planktonic tunicates) witnessed that the predatory action upon relatively large motile animals can be undertaken by sessile cnidarian species (Kruger & Griffiths, 1997; Orejas et al., 2001; Gili et al., 2006). "Sit-and-wait" predation is carried out by waiting for a prey to get in contact with the tentacles and the capture requires the discharge of nematocysts (Kruger & Griffiths, 1997; Thorington et al., 2010; Kaliszewicz, 2013). Differed from feeding upon relatively small prey, the capture of large animals involves numerous tentacles that simultaneously attach firmly to the prey, together with additional movements such as the extension and retraction of the column, bending of tentacles and wide opening of the mouth (Bos et al., 2011; Wickel et al., 2017; Sun et al., 2022). Description of multiple small polyps engaged in the collective capture of a large prey has been reported and referred to as protocooperation (Musco et al., 2018; Ter Horst and Hoeksema, 2021; Gregorin et al., 2022). Predation upon large animals requires high energetic costs, with presumably higher gain for the energetic budget (Carbone et al., 2007). The ability of polyps to shift from a low-cost predation upon small prey to a hard and enduring capture of large prey highlights an intriguing aspect of the evolution of predatory behaviour of sessile animals. Indeed, they are not able to actively hunt and search for food patches but show a wide feeding plasticity. Moreover, the success in large-prey capture by cooperating small polyps suggests a possible driver of non-cognitive formation of groups (sensu Ritz, 1994 on biological aggregations) and ultimately coloniality. Despite such evolutionary relevance, the extent of large-prey feeding has been so far neglected, being represented by punctual observations rather than by structural studies. Energetic models based on prey/predator size ratio exist for other animal taxa (Carbone et al., 2007) but are missing for sessile Cnidaria. This review aims to define the status of research on this topic, including both exclusively sessile species (Anthozoa) and those that spend a period of their life cycle as polyps (Medusozoa). This review allowed to produce a detailed framework of Cnidaria predating upon large animals, supplying information about involved species, their size ratio, lifestyle and trophism of predators, highlighting the feeding plasticity of Cnidaria species and their opportunistic trophic habits. The main outcome evidenced common features of large-prey feeding, highly different from those determined by the other trophic modalities, nonetheless lacking an attributable specific term. Thus, we suggest a unifying terminology for feeding modalities in relation to the size ratio between prey and predator, characterized by distinct behaviours and energetic requirements.

Materials and methods

The review was carried out following PRISMA 2020 Statement (Page et al., 2021). The research was made

using the Scopus (https://www.scopus.com) and Web of Science (WoS hereafter, https://www.webofscience.com) databases. The keywords combination tested were "Cnidaria" AND "large prey", "polyp" AND "large prey", "Anthozoa" AND "large prey" and "Cnidaria" AND ("large prey" OR "predation"), the latter resulting the most appropriate in both databases after looking at the outcomes of the other combinations (Fig. 1). All peer-reviewed publications, scientific manuscripts, pre-prints, conference papers, books and book chapters, and PhD theses, published until 31 December 2023 in English, Italian or Spanish, were included. All the documents reporting the searched terms in the title, keywords or abstract were scanned (Table 1). Manual research was further carried out by consulting citations and the references

section of the eligible publications, since the full read of the text highlighted the presence of documents not retrieved during the systematic research. The screening and eligibility of manually searched documents were based on the consistency of the citation in the text and on the title of the cited reference. This review exclusively considers the sessile stage (both temporary and permanent) of colonial and solitary species belonging to the phylum Cnidaria (i.e. the polyp) and focuses on the size of the prey, considered "large" when equal or major than the size of its predator. The size of a single polyp was considered for colonial organisms. Sizes of species involved in the description were extrapolated from web databases and scientific articles when not specified in the text (e.g. World Register of Marine Species, https://www.marinespec
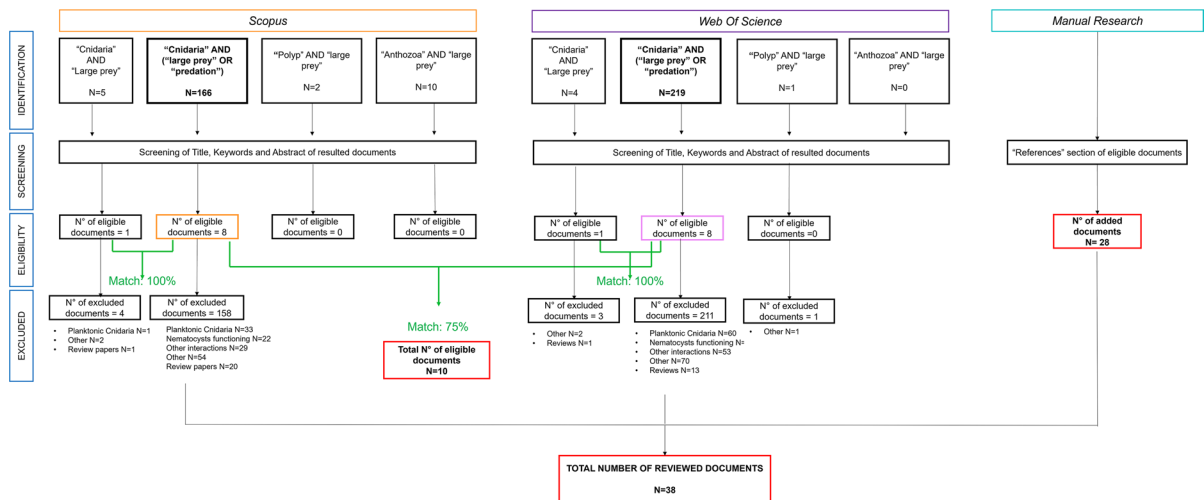
Fig. 1 Scheme of the literature research on Scopus and Web of Science databases, with reference to resulted, screened, eligible and excluded documents. Total number of manually added and reviewed documents is reported

Table 1 Inclusion and exclusion criteria for the selection of documents		
	Years	1900–2023 (last search: December 31, 2023)
	Database	Scopus and Web of Science
	Validated query (see Fig. 1)	"Cnidaria" AND ("large prey" OR "predation")
	Inclusion criteria	● Published documents, languages: English, Italian and Spanish ● Benthic or sessile life-stage of species of phylum Cnidaria ● Size of prey ≥ Size of polyp
	Exclusion criteria	● Duplicates manuscripts, reviews, other languages, referring to other topics ● Pelagic Cnidaria ● Size of large prey < Size of predator

ies.org). All the eligible documents (databases + manual addition) were screened and the full title, author list, year of publication and DOI were reported (Table 2). Additional information useful for the aim of the review was extracted from each document and converted in data (available as Supplementary Material at Table S1): (1) predator ID, including species name, taxonomic classification (Class and Order) and Author citation; (2) prey ID, including species name and taxonomic classification (Phylum and Class); (3) size ratio of predator based on the oral diameter of the single polyp and the prey; (4) lifestyle of predators (solitary or colonial species); (5) trophism of

predators (heterotrophic or mixotrophic); (7) behavioural description of predators (present or absent); (6) location of the survey, including Marine Realms and Ecoregions (Spalding et al., 2007); (7) type of survey (laboratory analysis, sampling and field observation or both); (8) depth at which field observations were made, referring to the light irradiance zonation of the water column [conventionally considered euphotic, from surface to −200 m (m); disphotic or twilight, from −200 to −1,000 m and aphotic, below −1,000 m; Letelier et al., 2004; Buesseler et al., 2007; Cerrano et al., 2019]; and (9) methods presented in the documents. Table S1, Supplementary

Table 2 General features of the eligible articles and features of interest for the review

| General features	
Category	Definition
File location	File location (where the document was found)
	(i) S: document present in Scopus database
	(ii) WoS: document present in Web of Science database
	(iii) S + WoS: document present in both databases
	(iv) M: manual adding
Year	Year of publication
Authors	Full list of authors of the publication
Title	Title of the publication
DOI	DOI of the publication or URL reference when DOI not available
Field	Field of the publication
Predator ID	Cnidarian species described to feed upon large prey followed by class, order, and author citation
Prey ID	Species of prey animals followed by phylum, class, and author citation
Size ratio of Predator:Prey	Ratio between the size of the individual predator and the prey. In case of colonial species, the average size of one polyp was used (< 1:10; 1:10–1:20; > 1:20)
Lifestyle of predator	(i) Colonial
	(ii) Solitary, free-living
Trophism of predator	(i) Mixotrophic
	(ii) Heterotrophic
Behavioural description	Presence or absence of behavioural description of benthic Cnidaria during predation upon large animals, for laboratory and field observations
Location	Location of the survey
Marine Realm	Marine realm to which the location belongs (Spalding et al., 2007)
Ecoregion	Ecoregion to which the location belongs (Spalding et al., 2007)
Type of survey	(i) Field observations and experiments (natural conditions)
	(ii) Laboratory experiments (controlled conditions), also including sampling activities
	(iii) Both
Method	Methodology used for the survey
Depth	Depth to which the survey was performed
Zone	(i) Euphotic (0 to −200 m)
	(ii) Disphotic (−200 m to −1,000 m)
	(iii) Aphotic (> −1.000 m)

Complete features are reported as Supplementary Material in Table S1

Materials, includes the complete list of reviewed documents along with the information on retrieval from database or manual research.

These data were elaborated by R software environment 4.2.2 Ink (RRID:SCR_000432; R Core Team, 2022) using the packages ggplot2 (Wickham, 2016) to show the spatial and temporal distribution of the searched articles and to graphically displaying publication targets, sampling strategies, study methods, taxonomy, and ecological traits of the studied species.

Results

The number of documents resulting from the systematic research on Scopus database with the keywords "Cnidaria" AND ("large prey" OR "predation") was 166, of which 8 were considered eligible after the screening following the inclusion and exclusion criteria. The other 158 documents were excluded because review papers focusing on different topics ($N=20$) or dealing with other topics (pelagic Cnidaria: $N=33$; Nematocysts functioning: $N=22$; Inter- or intraspecific interactions other than predation by benthic Cnidaria: $N=29$; Other: $N=54$, Fig. 1). The number of results obtained with the keywords "Cnidaria" AND "large prey" was 5, of which 1 considered eligible and matching one result obtained from the above-mentioned query (Total of Scopus results $N=8$). From Web of Science, the same keywords combination ["Cnidaria" AND ("large prey" OR "predation")] resulted in the highest number of documents ($N=219$), of which 8 were considered eligible (Fig. 1). Six documents were present in both databases (match$=75$%), for a total of 10 eligible documents outlined from the systematic research. Continuing with the complete reading of the 10 eligible documents, additional 28 scientific articles cited in the text were identified and screened. In total, 38 publications have been here reviewed (Fig. 1). The first study was published in 1970, while the most recent was published in 2022. The interest on this topic showed an increasing trend through the years (Fig. 2), with the maximum number of documents reached in the 2010s ($N=17$), while the first 4 years of 2020s (2020–2023) counted six publications ($N=6$), prospecting a greater number of reports by the end of the decade although no documents were published in 2023.
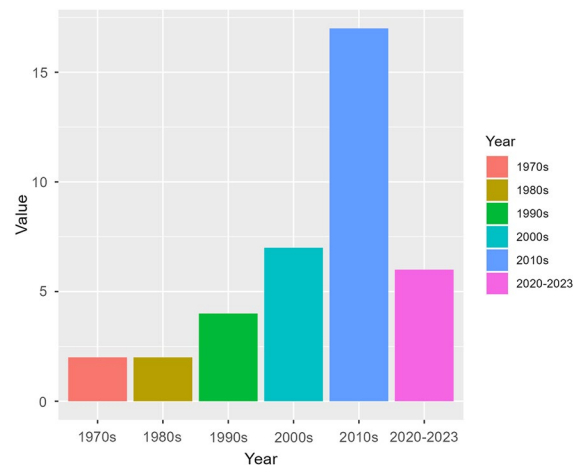
Fig. 2 Temporal distribution of the 38 eligible studies on cnidarians feeding upon large preys displayed as number of publications per decades from 1970 to 2023 (1970s: 1970–1979, 1980s: 1980–1989, 1990s: 1990–1999, 2000s: 2000–2009 and 2020 to the last search on 31 December 2023). Data elaboration: R environment (R Core Team, 2022)

Regarding the spatial distributions of the 38 reviewed articles (Fig. 3), the reports are homogeneously distributed in different geographic areas (Fig. 3). The highest number of reports is derived from the marine realms of Temperate Northern Atlantic ($N=8$ studies, 22%, Fig. 3 and 3a, yellow) with the ecoregions Western Mediterranean ($N=5$), Southern Norway (N=1), North Sea ($N=1$) and Celtic Sea ($N=1$). Such a figure was followed by Central Indo-Pacific ($N=7$, 19%, Fig. 3 and 3b, orange) with ecoregions Eastern Philippines ($N=2$), Palawan/North Borneo ($N=2$), Gulf of Thailand ($N=2$) and Western Caroline Islands ($N=1$). Finally, the Southern Ocean ($N=7$, 19%, Fig. 3 and 3c, blue) encompasses the ecoregions of Ross Sea ($N=4$) and Weddell Sea ($N=3$). Only one publication was reported on a freshwater cnidarian species located in the Nahuel Rucá Lake, Argentina (Deserti et al., 2017) (Fig. 3, black star). Information on field location was not available in four documents ($N=4$), which reported laboratory analyses or because out of the limit of the ecoregions.

Regarding to the ecological aspects, most publications focused on trophic ecology of cnidarians, describing their feeding modalities ($N=33$ articles, 86%), although large-prey capture and ingestion were also reported as a side-observation while describing
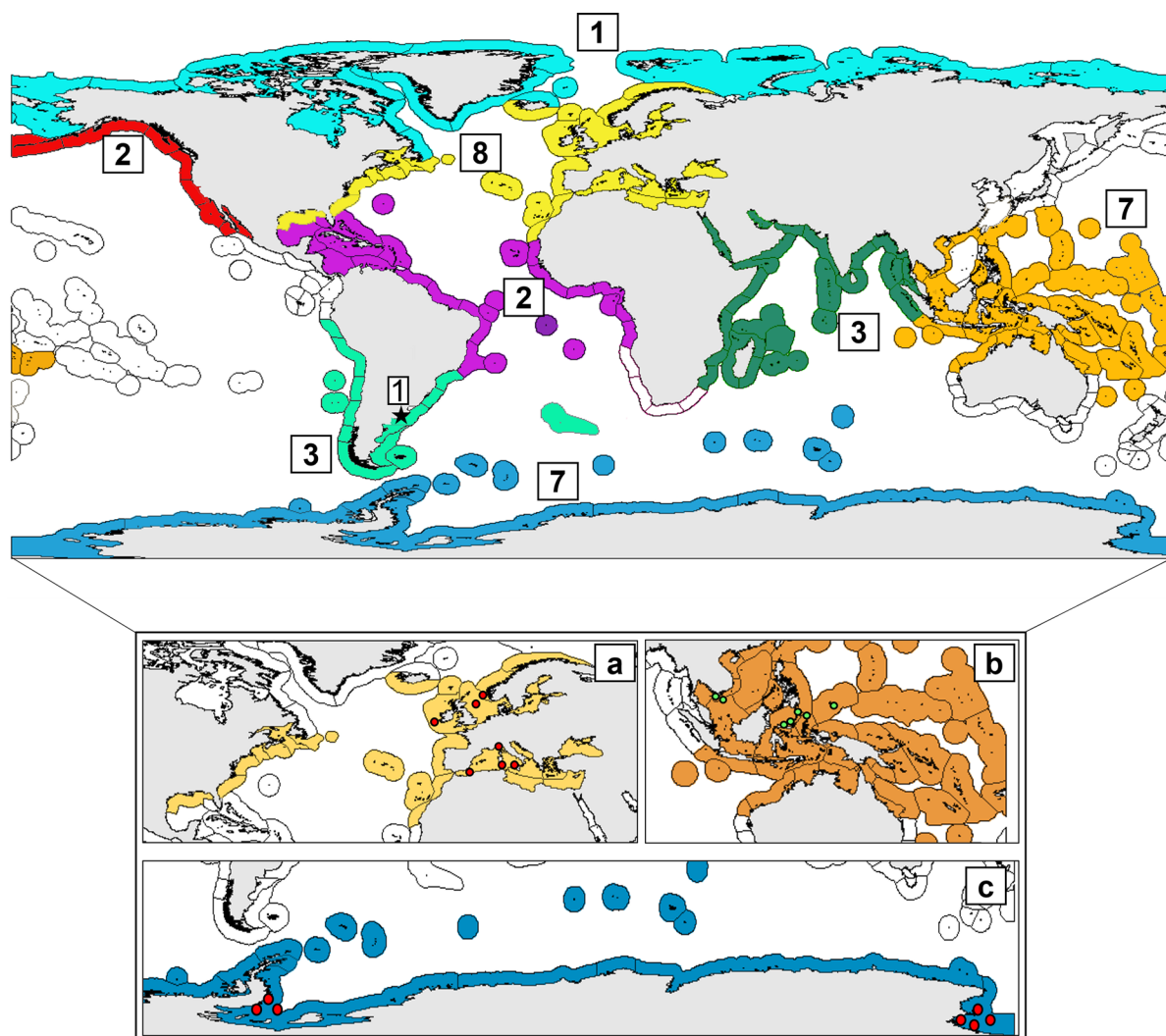
Fig. 3 Number of publications per marine realm (Spalding et al., 2007). Temperate Northern Atlantic ($N = 8$, yellow); Central Indo-Pacific ($N = 7$, orange); Southern Ocean ($N = 7$, blue); Western Indo-Pacific ($N = 3$, dark green); Tropical Atlantic ($N = 2$, purple); Temperate Northern Pacific ($N = 2$, red); Temperate South America ($N = 3$, light green); Arctic ($N = 1$; light blue); Freshwater ($N = 1$, black star). Not Available: $N = 3$. In **a–c** marine ecoregions; **a** Tropical Northern Atlantic realm, ecoregions of Western Mediterranean, Celtic Sea, North Sea and Southern Norway, **b** Central Pacific Ocean realm, ecoregions of West Caroline Islands, Eastern Philippines, Palawan/North Borneo, Gulf of Thailand, and **c** Southern Ocean, ecoregions of Ross Sea and Waddell Sea

the species ($N = 3$, 8%) or the habitat (N $= 2$, 5%, Fig. 4a).

The most used sampling methodology was based on recording of the predatory action through underwater photos and videos ($N = 15$, 40%), followed by gastric content analysis ($N = 8$, 21%). In general, most observations and experiments were carried out in the sea ($N = 20$, 53%), followed by sampling for posterior analysis and laboratory trials ($N = 12$, 31%)

or both ($N = 5$, 13%). Data were not available in one document ($N = 1$, 3%, Fig. 4b). The higher number of manuscripts describing natural observations of the predatory action were reported by video or photorecordings (ROV/vehicles: $N = 3$, 15%; Underwater operator: $N = 5$, 25%; Other, e.g. time-lapse camera: $N = 12$, Fig. 5).

About the bathymetrical distribution of the field research, out of the total field observations and
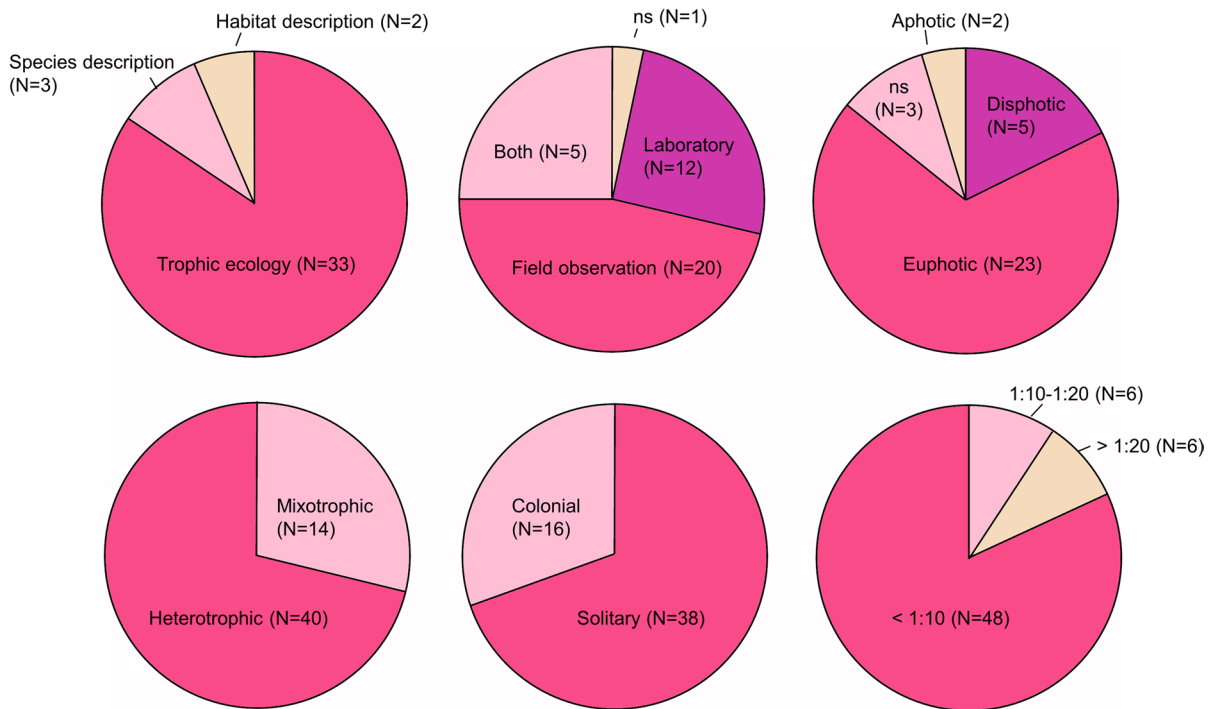
Fig. 4 a Field of study of the publications reporting large-prey predation by cnidarian polyps, **b** type of survey: field observations or experiments, sampling and laboratory processing of samples or laboratory trials, both methodologies; *ns* not specified/available, **c** whether in the field, zone in which the survey was carried out; this information was extrapolated basing on he survey's depth; *ns* not specified/available, **d** feeding habits of cnidarian species, **e** lifestyle of cnidarian species and **f** size ratio of predator (single cnidarian polyp's size) and prey species. Some data fall into more categories as the size range is provided. Elaboration in R environment (R Core Team, 2022)
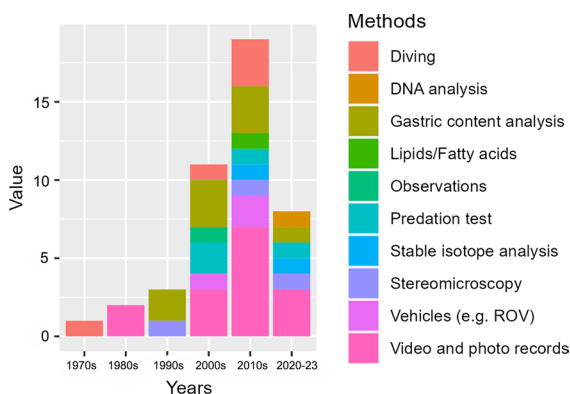
Fig. 5 Types of the methods for the study of large-prey capture and ingestion across decades from 1970 to 2023 (1970s: 1970–1979, 1980s: 1980–1989, 1990s: 1990–1999, 2000s: 2000–2009 and 2020 to the last search on 31 December 2023). *ROV* remotely operated vehicle. Elaboration in R environment (R Core Team, 2022)

sampling depths ($N=30$), 22 were made in the euphotic zone (73%, e.g. Moraes & Chagas-Júnior, 2009; Wickel et al., 2017), ranging from the surface to 200 m depth, of which 18 were above 20 m depth and 5 were below 20 m depth. However, the reports of large-prey predation by benthic Cnidaria were also reported in the disphotic ($N=5$, 17%, e.g. Jarms & Tiemann, 2004; Sun et al., 2022) and aphotic ($N=2$, 7%; Lampitt & Paterson, 1987; Durden et al., 2015) zones down to the oceanic abyssal plain at 4,850 m depth (Fig. 4c).

The number of benthic cnidarians described while predating upon large prey was 54, with 13 species described by more than one document (e.g. *Astroides calycularis* (Pallas, 1766) by Musco et al., 2018 and Cerrano et al., 2016; *Anthomastus bathyproctus* Bayer, 1993 by Orejas et al., 2001, Gili et al., 2006 and Elias Piera, 2015; *Entacmaea medusivora* Fautin & Fitt, 1991, Fautin & Fitt, 1991 and Hoeksema et al., 2015). Among the 51 descriptions (species, genera or

taxa indicated), 40 are heterotrophic (74%) and 14 are mixotrophic (26%, Fig. 4d). The heterotrophic category includes the deep-sea anemones *Isotealia antarctica* Carlgren, 1899 (Dayton et al., 1970), *Iosactis vagabunda* Riemann-Zürneck, 1997 (Durden et al., 2015), *Actinostola callosa* (Verrill, 1882) (Jarms & Tiemann, 2004) and shallower species, among which the scleractinian *Leptopsammia pruvoti* Lacaze-Duthiers, 1897 (Cerrano et al., 2016) and *Tubastraea* cf. *micranthus* (Ehrenberg, 1834) (Gregorin et al., 2022). Mixotrophic species needs light to sustain the symbionts hosted in their tissue, such as the species *Montastraea cavernosa* (Linnaeus, 1767) (Ter Horst & Hoeksema, 2021), *Aiptasia* sp. (Ou et al., 2022) and *Anemonia sulcata* (Pennant, 1777) (Canovas & González-Wangüemert, 2018). No chemoautotrophic species were described by any paper while ingesting large prey. Anthozoa is the most reported cnidarian class that predates upon large animals (*N*=47, 87%), with representatives of each order (Actinaria, *N*=27 species, 57%; Scleractinia, *N*=11, 23%; Corallimorpharia, *N*=3, 6%; Scleralcyonaria, *N*=3, 6%; Zoantharia, *N*=2, 4%; Antipatharia, *N*=1, 2%), while the class Hydrozoa was entirely represented by the few millimetres size *Hydra* genus, order Anthoathecata (*N*=6, 11%). Only one report involved the polyp stage of *Aurelia coerulea* von Lendenfeld, 1884, Scyphozoa Semaeostomeae (*N*=1, 2%, Fig. 6a). Most of these species are solitary (*N*=37, 68%), e.g. the

actinarians *I. antarctica*, *U. antarctica* (Verrill, 1922), *Sagartia lacerata* (Dalyell, 1848) and *E. medusivora*, while others are colonial (*N*=16, 30%), e.g. *A. calycularis*, *M. cavernosa*, *Madracis auretenra* Locke, Weil & Coates, 2007, *Meandrina meandrites* (Linnaeus, 1758) and *Anthomastus bathyproctus* (Fig. 4e).

The analysis of the prey individuals (*N*=61) indicated that jellyfish (Cnidaria, Scyphozoa) were the most predated taxon (*N*=16 descriptions, 26%) both in shallow and in deep environments (e.g. Barryman, 2984; Fautin & Fitt, 1991; Gili et al., 2006). The second most predated taxon was Echinodermata (*N*=13, 22%) with the classes Asteroidea (*N*=7, 54%, e.g. Bos et al., 2008), Echinoidea (*N*=4, 31%; e.g. Dayton et al., 1970), Ophiuroidea (*N*=1, 8%; Sun et al., 2022) and Holothuroidea (*N*=1, 8%; Bos et al., 2011), followed by Mollusca (*N*=13, 21%; Gastropoda *N*=8, 67%, Kruger & Griffiths, 11997 Mehrotra et al., 2019; Bivalvia *N*=4, 31%; Acuña-Maurizio & Zomponi, 1996; Cephalopoda *N*=1, 8%, Lampitt & Paterson, 1987), Tunicata Thaliacea (*N*=7, 12%, single or as chains of planktonic tunicates, e.g. Porter, 1974; Orejas et al., 2001), Annelida (*N*=5, 8%: Polychaeta *N*=4, 80%, e.g. Bavestrello et al., 2000; Oligochaeta *N*=1, 20%, Moralse et al., 2018), Arthropoda (*N*=4, 7%; Crustacea *N*=3, 75%, e.g. Deserti et al., 2017; Chilopoda *N*=1, 25%, Moraes & Chagas-Júnior, 2009), Chordata (*N*=2, 3%: Teleostei *N*=1, 50%, Ivanova
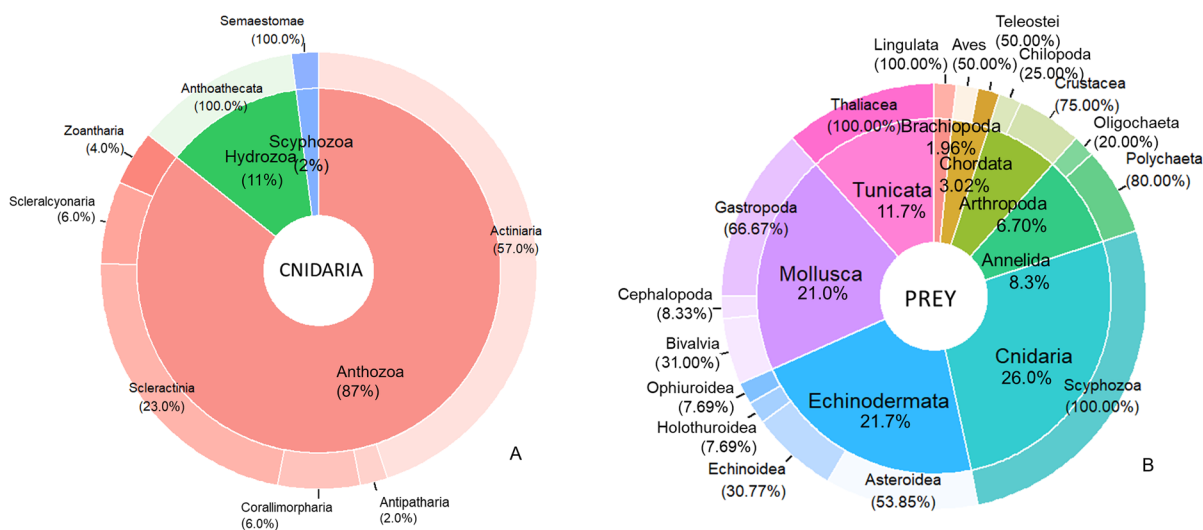
Fig. 6 **a** Class and Order of predatory cnidarian species and **b** Phylum and class of prey species. Elaboration in R environment (R Core Team, 2022)

& Grebelnyi, 2017; Aves $N = 1$, 50%, Sheffield Guy et al., 2014) and Brachiopoda ($N = 1$, 2%, Fig. 6b).

Behavioural observations

Surveys involving direct observation by SCUBA divers, video and photorecords, the use of underwater vehicles and laboratory predation tests (total: $N = 28$) were evaluated in order to assess the presence or absence of behavioural description of predating polyps. Among these, the detailed description of behaviour of the capture was provided in 16 documents. Reports evidenced the detection of the prey by mean of tentacles ($N = 16$), the shortening or bending of the tentacles to pull the prey towards the gastrovascular cavity ($N = 14$) and the wide opening of the mouth to engulf the large prey or parts of it ($N = 9$). In six documents, the exploitation of the large prey was carried out by multiple polyps simultaneously (e.g. Fautin & Fitt, 1991; Bavestrello et al., 2000; Musco et al., 2018). Description of the total or partial ingestion of the prey was reported in nine (Mehrotra et al., 2016; Sun et al., 2022) and five documents (e.g. Mehrotra et al., 2019; Huang et al., 2020), respectively. The handling time (i.e. the time spent by predator from the first contact with the prey to the total ingestion/loss/rejection of the prey) was reported in three documents, for a duration of minimum of 10 min (Mehrotra et al., 2019) and maximum of 16 h (Durden et al., 2015). The digestive phase was mentioned in five documents, indicating the total prey consumption within 56 h ($N = 1$, Durden et al., 2015) and 24 h ($N = 1$, Tang et al., 2020), and the digestion of soft tissues and rejection of prey remains, including indigestible parts (e.g. spine and plates of sea urchins, shell of molluscs, e.g. Bos et al., 2011) and consumed tissues ($N = 3$, e.g. Mehrotra et al., 2019). In eight documents, the fate of the prey was evidenced: death ($N = 2$, e.g. Durden et al., 2015), escape through autotomy of predated parts ($N = 1$, Bos et al., 2008), escape due to advantages (speed, size, grip with the substrate for vagile benthic species) ($N = 3$, e.g. Bos et al., 2011), escape due to wave action and strong current ($N = 1$, Mehrotra et al., 2019) and scavenging by other animals during handling time ($N = 1$, Fautin & Fitt, 1991).

Discussion

The main outcome of this review emphasizes that the predatory relationship between benthic Cnidaria (Anthozoa in particular) and large prey is a distinct feeding modality. It is not influenced to specific features of the environment (e.g. depth, temperature, light irradiance), nor of the species trophism and lifestyle. Rather, it is related to the identity of the prey and on the size ratio between prey and predator. The predation upon large animals should be considered as an opportunistic feeding modality (Acuña & Zamponi, 1995; Orejas et al., 2001; Alamaru et al., 2009; Musco et al., 2018), as witnessed also by the engulfing of terrestrial animals occasionally fallen in the sea (Moraes & Chagas-Júnior, 2009; Sheffield Guy et al., 2014). The behaviour of polyps during capture of the large prey is described in most surveys on alive animals. It requires specific body movements, including stretching of column and mouth (up to 400% of original size; Barryman 1984), bending of tentacles and long-lasting handling time and engulfment (up to 4 h; Canovas & González-Wangüemert, 2018). Conversely, the ingestion and digestion phases are seldom reported. This gap is probably due to the long time required for observation, up to 16 h for complete ingestion and 56 h for complete digestion (Durden et al., 2015). The fate of the prey describes four different scenarios: (1) death following multiple predator attacks (Huang et al., 2020) or total ingestion (e.g. Sun et al., 2022); (2) prey escape through autotomy of body parts (e.g. Bos et al., 2008); (3) escape due to wave motion and current that carry the prey away from predator (Mehrotra et al., 2019), or due to sufficient large body size and speed (Bos et al., 2011); and (4) release, when the predator loses the grip on the prey (Bos et al., 2008), or it is satiated (Gregorin et al., 2022). During handling time, possible kleptopredation occurs, as observed by Hoeksema et al. (2015) and suggested by Bavestrello et al. (2000).

An increasing trend of publications can be noticed from the 1970s to present days, reflecting a rising interest in trophic ecology of benthic communities including sessile cnidarians. This result confirms the previous findings of Santos et al. (2020), which also reported an increasing number of publications dealing with feeding in Anthozoa starting from the 1970s. The availability of user-friendly and low-cost action cams could have facilitated the underwater

data recording and spurred studies on animal behaviour. Indeed, most used methodology in the euphotic zone involved the deployment of underwater cameras, or manually recorded videos through SCUBA diving (e.g. Mehrotra et al., 2016; Wickel et al., 2017; Canovas & González-Wangüemert, 2018; Musco et al., 2018; Gregorin et al., 2022). Following the growing interest towards the global change scenario, the attention of the scientific research has been directed towards coral reefs and coastal ecosystems worldwide. These ecosystems are highly biodiverse and extremely sensitive to temperature increase (Hoegh-Guldberg, 2011a; Harvey et al., 2018; Lu et al., 2018; He & Silliman, 2019; Goreau & Hayes, 2021) and anthropogenic impacts (Hoegh-Guldberg, 2011b; Huang et al., 2021; Reverter et al., 2022). The widespread distribution of the observations indicates that large-prey predation is a common modality not linked to specific latitudes, habitats or physical and chemical features of the seawater. This feeding strategy could be related to the availability of resources, i.e. the distribution and abundance of food items. Analogously, seasonal differences in gastric contents were found in *Phymactis clematis* (Drayton in Dana, 1846)*, Aulactinia marplatensis* (Zamponi, 1977) and *Bunodactis reynaudi* (Milne Edwards, 1857), suggesting seasonal variation of prey availability. These outcomes were further confirmed by the similarity of gastric contents among samples from different locations in the same season (Acuña & Zamponi, 1995). Benthic Cnidaria, mostly Anthozoa Actinaria, are involved in predatory relationships with many large-prey taxa. Similarly, Santos et al. (2020) reported Actinaria, followed by Scleractinia, as the cnidarian groups most recorded in their review dealing with feeding in Anthozoa. The most abundant prey taxon is represented by scyphozoans (Cnidaria), i.e. jellyfish (e.g. Hoeksema et al., 2015; Cerrano et al., 2016). Most documents on benthic cnidarians feeding upon jellyfish reported mass occurrences of the latter due to seasonal blooms, diel vertical migrations or due to the absence of competitors and favourable conditions (e.g. Fautin & Fitt, 1991; Orejas et al., 2001; Gili et al., 2006; Musco et al., 2018; Ter Horst & Hoeksema, 2021), as in the case of the Jellyfish Lake, Palau, West Caroline Islands (Fautin & Fitt, 1991) and Lake Kakaban, East Kalimantan, Indonesia (Hoeksema et al., 2015). The size ratio between preys and predator is seldom greater than 20 to 1. In most predatory interactions described, the prey size appears from equal up to 10 times larger than the oral disc of the single polyp. However, the size of prey and predators is often not reported, and for some groups (e.g. Actinaria), the diameter of the individual is measured at the basal disc instead of the oral disc (e.g. Acuña-Maurizio & Zomponi, 1996). However, the latter could be the most representative for the feeding ability, and more accurate measure for other groups, e.g. colonial polyps, hydroids and scyphozoans (e.g. see Gambill & Jarms, 2014). The benthic cnidarian species engaged in large-prey predation encompassed both solitary [e.g. *E. medusivora*, Fautin & Fitt, 1991; *Anthopleura xanthogrammica* (Brandt, 1835), Sheffield Guy et al., 2014 *Paracorynactis hoplites* (Haddon & Shackleton, 1893), Wickel et al., 2017] and colonial forms (e.g. *A. bathyproctus*, Orejas et al., 2001; *M. aburetenra*, *M. meandrites*, Ter Horst & Hoeksema, 2021). Solitary species were characterized by larger oral diameters or longer tentacles than colonial polyps. The average prey/predator size ratio was 1:4.6 ± 4.7 SD for the solitary polyps and 1:11.8 ± 10.1 for the colonial ones. Coloniality allowed polyps to share the capture of the large prey, as observed by Musco et al. (2018), Ter Horst & Hoeksema (2021) and Gregorin et al. (2022). Albeit previously documented (e.g. Cerrano et al., 2000), the collective capture performed by relatively small polyps was firstly proposed by Musco et al. (2018) as protocooperation. These last authors described the colonial stony coral *A. calycularis* feeding upon the mauve stinger *Pelagia noctiluca* (Forsskål, 1775), up to 12 times larger than the oral disc of the single polyp (Musco et al., 2018). Protocooperation refers to the non-obligatory mutualistic relationship between two or more organisms that receive benefit but are not dependent from each other (Skelton, 1979; Herbert-Read et al., 2016) and could be potentially performed by polyps in facultative aggregations. Here, protocooperating polyps benefit from the collective capture, which eventually result in successful feeding upon a large prey. Group-foraging is highly advantageous and widely spread among animal taxa (Clark & Mangel, 1986). Together with other benefits of group-living (e.g. predator defence, higher mating chances and enhanced survival), group-foraging allows to access to food resources hardly or not achievable by the single individual (Krause & Ruxton, 2010).

The predation of large animals was observed at all depths, from the euphotic (e.g. Ter Horst & Hoeksema, 2021; Gregorin et al., 2022) to the disphotic (e.g. Elias Piera, 2015) and aphotic zones (e.g. Lampitt & Paterson, 1987), characterized by different light irradiances. However, the number of studies in the latter two zones was limited, plausibly due to the greater difficulty in exploring deep ecosystems (Amon et al., 2022). Thus, available reports on deep species may not represent a reliable picture of the extent of large-prey exploitation by benthic cnidarians, often dominant in the deep-sea benthic communities (Jarms & Tiemann, 2004). The results suggest that depth is not a limiting factor, and that the trophism (heterotrophy vs. mixotrophy) of the reported cnidarian species does not influence their ability to catch large prey (Cerrano et al., 2019). However, heterotrophic species were more abundant than mixotrophic ones. This result could support the hypothesis that heterotrophic species might be encouraged to engage in predation upon large animals more than mixotrophic ones, because of lacking nutrients from photoautotrophic origin. However, this speculation should be confirmed by further observations and laboratory assays.

The most reported prey animals belonged to the taxonomic groups of Cnidaria Scyphozoa and Tunicata Thaliacea, being part of the gelatinous zooplankton. These organisms form seasonal swarms for mating purposes or as a result of patchy food availability (Purcell et al., 2007; Henschke et al., 2016; Groeneveld et al., 2020; Décima et al., 2023). Nowadays, it is recognized that gelatinous zooplankton highly contributes to the organic carbon and nutrient cycles in many ecosystems. "Jelly falls" and "salps falls" refer to mass sinking of moribund or dead gelatinous zooplankton, which represent major food resources for many benthic species (Sweetman & Chapman, 2011; Henschke et al., 2013; Lamb et al., 2017; Tinta et al., 2020; Wright et al., 2021; Licer et al., 2023). While alive, the swarms of gelatinous zooplankton produce high quantity of sinking faecal pellets that enter the benthic biogeochemical cycle (Iversen et al., 2017; Pauli et al., 2021). Gelatinous zooplankton has, for long time, been considered as a trophic endpoint in the pelagic ecosystem (Henschke et al., 2016; Lamb et al., 2017), but the link between pelagic and benthic organisms reveals its importance in the trophism of many benthic species. Thus, jellyfish predation

performed by cnidarian polyps should be considered as further important pathway of the benthic–pelagic coupling (Orejas, 2001; Gili et al., 2006).

A general comment on the systematic review herein performed is required to emphasize the difficulty in identifying documents on the topic object, as well as to stress the need to standardize the terminology in taxonomical and ecological research (Di Camillo et al. 2018, 2023). The research on the Scopus and Web of Science databases produced a low number of outcomes for all the tested combinations of keywords, except for "Cnidaria" AND ("large prey" OR "predation"). Only 8 over 166 and 219 documents (respectively) resulted eligible for the purposes of the review, while the manual research returned 28 documents, more than triple. Most of the excluded documents were out of topic or referring to planktonic Cnidaria. Such paucity of eligible papers is attributable to the absence of a standard terminology for describing the predation and consumption of prey larger than the single polyp. The most abundant food resources for benthic cnidarians are dissolved and particulate organic matter, and organisms from pico- to mesoplankton (Sieburth, 1978; Houlbrèque & Ferrier-Pagès, 2009). Despite being widely neglected, this review highlighted that the feeding upon large motile animals could be more common than expected and relevant in the ecology of benthic Cnidaria. Moreover, in some excluded documents, the "large" or "larger" prey was not larger than the predator size, thus not requiring different feeding behaviour of that for smaller organisms. These discrepancies in the use of terms suggest that an agreed terminology should be defined. The term "suspension-feeding" refers to a passive feeding modality through which polyps absorb dissolved organic matter (e.g. exudates, urea, dissolved free amino acids), or ingest detrital particulate organic materials (e.g. faecal pellets agglomerates of microalgae, bacteria) falling within their crown of extended tentacles (Rossi et al., 2004; Houlbrèque & Ferrier-Pagès, 2009). This modality does not require nematocysts discharge nor active movements of the polyp, but the direct assimilation of nutrients (Schlichter, 1982). "Sit-and-wait" predation occurs when an alive prey, freely swimming in the water column or moving on the substrate (generally on the side of the polyp, Sun et al., 2022), reaches the tentacle(s) and it is captured. Predation involves the release of nematocysts that block and often kill the
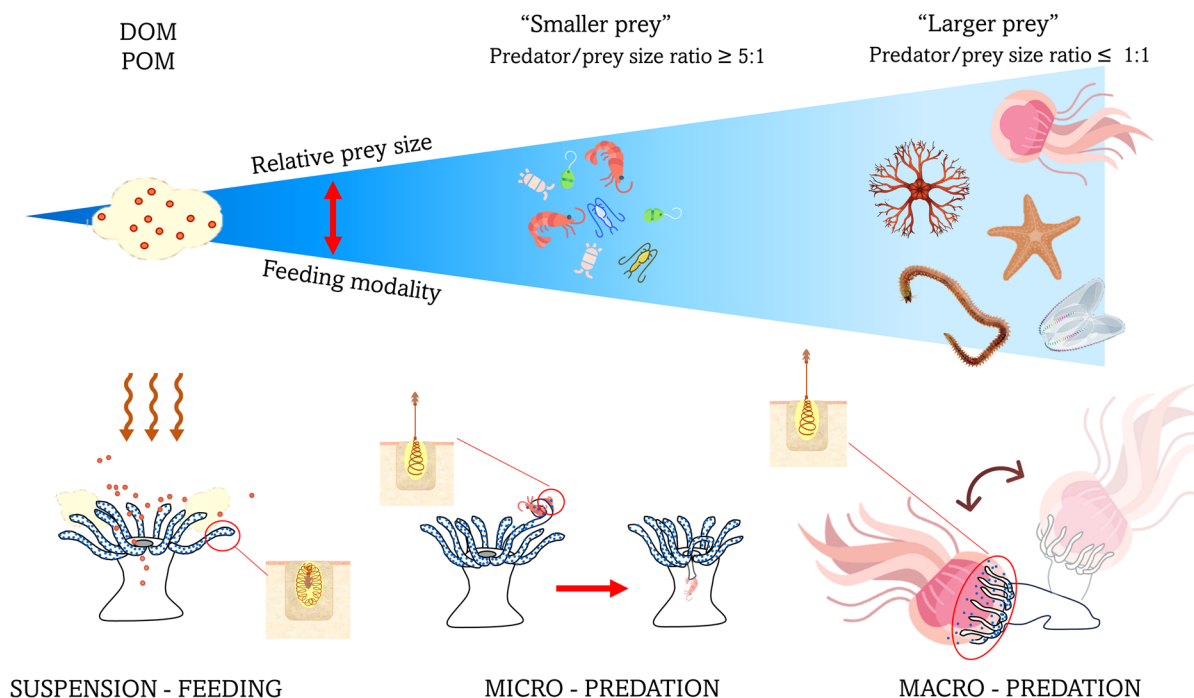
Fig. 7 Proposed terminology referred to the behaviour of polyps and the size ratio between predator polyp and its prey. *DOM* dissolved organic matter, *POM* particulate organic matter. The indicated size ratios determine the different heterotrophic feeding behaviour (suspension-feeding, micro- or macro-predation). Suspension-feeding does not require nematocysts (blue dots) discharge. In micro- and macro-predation, the nematocysts discharged for the capture of the prey in correspondence with the contact between the prey and the tentacle(s)

prey, then transported to the oral opening by tentacles (Kaliszewicz, 2013). A further distinction based on the size ratio between prey and predator is needed since it determines two distinct predatory behaviours. "Micro-predation" should refer to the capture of a relatively small prey if compared to the size of the predator. Such feeding modality requires the action of one tentacle that releases nematocysts only at the contact area. The energetic costs for nematocysts discharge and replacement are limited, as well as the amount of energy intake from the small prey. Generally speaking (not considering species-specificity and environmental conditions), this modality is not energetically expensive but requires a high number of prey items to satisfy the daily energetic demand. Instead, when the prey is relatively large, its capture requires many tentacles simultaneously, a massive discharge of nematocysts along all their length, and a long handling time with active pulling and stretching. The mouth opens widely to start prey ingestion of portions of the alive prey, often showing extracoelenteric digestion.

The prey tries to escape, and the tentacles are firmly attached on it until paralysis occurs. Ingestion phase lasts for many minutes (to more than 40, Jarms & Tiemann, 2004). The body can stretch towards the prey and change its shape after the ingestion or the prey release, becoming roundish and probably indicating a post-ingestion phase (e.g. Cerrano et al., 2000; Jarms & Tiemann, 2004; Wickel et al., 2017; Sun et al., 2022). Further, the polyp is engaged in the predation of a single prey item per time. The modality involving this peculiar behaviour should be referred to as "macro-predation", energetically expensive but providing a great reward in terms of energy intake. Some authors referred to the ingestion of large gelatinous zooplankton as "medusivory" (e.g. Jarms & Tiemann, 2004; Hoeksema et al., 2015), "salpivory" (e.g. Ter Horst & Hoeksema, 2021) and "jellyfish-eating" (e.g. Fautin & Fitt, 1991; Cerrano et al., 2016), posing the identity of the prey as pivotal. However, behavioural differences due to the type of large prey were not evident from the review. A generic indication

about the size ratio between predator (oral diameter) and prey (major dimension) could assist in the definition of the feeding behaviour, since the size of the prey will determine how the predator will engage in predation. We suggest a predator/prey size ratio $\leq 1:1$ for macro-predation and $\geq 5:1$ for micro-predation, as extrapolated by the screening of the excluded documents resulted from Scopus (see Fig. 7). We further recommend referring to the diameter of the oral disc rather than the basal disc, when possible, to standardize the dimension for all cnidarian taxa. Macro-predation could be performed by a single relatively large predator (e.g. giant green sea anemones, Rifa'i (2016); Sheffield Guy et al., 2014) or collectively by small-sized protocooperating polyps (e.g. hydroids; Cerrano et al., 2000). In conclusion, when analysing the feeding modality of benthic cnidarians, other than the prey identity and its dimension, papers should also report the predator/prey size ratio and the predator's feeding behaviour, to have a clear view of the feeding modality performed. This distinction will help to evaluate the extent of macro-predation and its ecological and evolutionary importance for the trophic ecology of sessile species.

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Data availability Data have been provided as Supplementary Materials.

Declarations

Conflict of interest The authors declare no conflict of interest.

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