Prey-capture rates in four Mediterranean cold water corals

Georgios Tsounis[1,*], Covadonga Orejas[1,2], Stéphanie Reynaud[3], Josep-Maria Gili[1], Denis Allemand[3], Christine Ferrier-Pagès[3]

[1]**Institut de Ciències de Mar (CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain**
[2]**Centro Oceanográfico de Santander (IEO), Promontorio de San Martin s/n, 39004 Santander, Cantabria, Spain**
[3]**Centre Scientifique de Monaco, Avenue Saint-Martin, 98000 Monaco (Principality)**

ABSTRACT: Little is known about the basic biology of deep-water coral species. In this study, we experimentally assessed the rates of ingestion of *Artemia salina* adults and nauplii by the 4 Mediterranean cold water coral species *Dendrophyllia cornigera*, *Desmophyllum cristagalli*, *Madrepora oculata*, and *Lophelia pertusa*. All species ingested *A. salina* in adult and nauplii forms. *L. pertusa* showed the highest grazing rate for both prey types, whereas *M. oculata* showed the lowest capture rates among the 4 species, and was practically unable to ingest adult prey. Capture rates of the 4 coral species ranged between 5 and 8 adult *A. salina*, and 50 and 280 nauplii $polyp^{-1} h^{-1}$. Surprisingly, both capture rates and carbon uptake (adult *Artemia* ingestion: 994 to 3542 µg C $polyp^{-1} h^{-1}$; nauplii ingestion: 78.1 to 462 µg C $polyp^{-1} h^{-1}$) were within the range of values found in some tropical corals (which often ingest 0.004 to 3600 prey items $polyp^{-1} h^{-1}$). The results show that the capture rates and energy input of the studied cold water coral species appear to be on a level that is comparable to that of other corals, even tropical zooxanthellate species.

KEY WORDS: Cold water corals · Grazing rates · Colony size · Trophic ecology · Benthic-pelagic coupling

INTRODUCTION

Cold water coral (CWC) communities are receiving increased attention as they support rich biodiversity and high fish abundances (Auster 2007, Spencer et al. 2007). However, little is known about the basic biology of deep-water coral species, in terms of growth rates, life cycle, and feeding.

Corals in general can meet their energy demands in a number of ways (Lasker 1981, Sebens & Koehl 1984, Freiwald 1998, Gili & Coma 1998, Orejas et al. 2001), and studies mostly performed on tropical corals have shown that they are able to prey on zooplankton (Muscatine & Porter 1977, Sebens 1987), phytoplankton (Fabricius 1998), pico-nanoplankton (Al-Moghrabi et al. 1993, Houlbrèque et al. 2004b), and dissolved organic matter (Grover et al. 2008). Energy can also be gained through zooxanthellae photosynthesis in sym-

biotic species (Muscatine 1990, Fabricius & Klumpp 1995, Houlbrèque & Ferrier-Pagès 2009), or possibly through ingestion of chemosynthetic bacteria in cold-seep species (Hovland et al. 1998, Hovland & Risk 2003).

No direct estimates of grazing rates in CWC are available at this time, but stochiometric analysis of the CWC *Lophelia pertusa* and *Madrepora oculata* from the Atlantic suggested that they might be omnivores rather than exclusive herbivores (Roberts et al. 2003, 2006), and might even feed primarily on mesozooplankton (Duineveld et al. 2004, Kiriakoulakis et al. 2005). Observations during research dives by manned submersible confirmed the abundant presence of zooplankton over CWC communities (Fig. 1). Zooplankton is an energy-rich food source that can, even in tropical zooxanthellate corals, significantly increase growth rates (Houlbrèque et al. 2003, 2004b). In fact, CWC
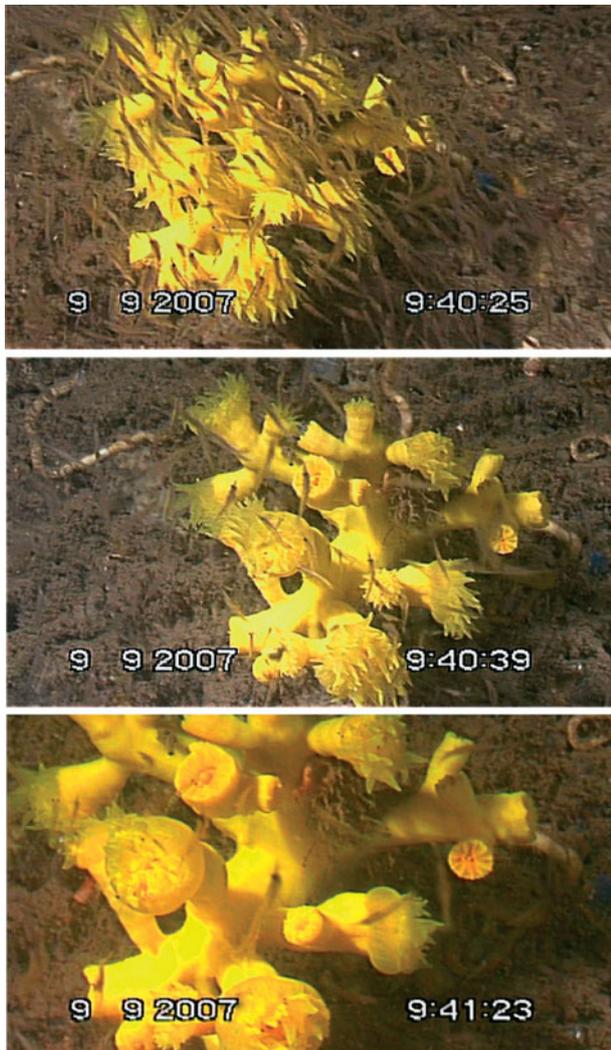
Fig. 1. Still frames from a video sequence that shows the occurrence of Euphausiacea shrimp over a colony of *Dendrophyllia cornigera*. Note that the density is increased by the effect of the lights on the submarine. See Video clips 1 and 2 in the supplement at www.int-res.com/articles/suppl/m398 p149_app/ Photo by JaGO-Team/IFM-GEOMAR Kiel

maintained with zooplankton diets in aquaria grow at rates that are comparable to some tropical corals (Orejas et al. 2008), further highlighting the importance of this prey type.

Given the availability and potential importance of zooplankton as CWC prey, we assessed capture rates of zooplankton by 4 characteristic Mediterranean CWC species under laboratory conditions.

MATERIALS AND METHODS

Four species of ahermatypic scleractinian CWC were collected at 150 to 250 m depth at the Cap de

Creus Canyon (Gulf of Lyons, NW Mediterranean) and off the Island of Malta: *Dendrophyllia cornigera*, *Lophelia pertusa* (collected in September 2007 at 42° 23.187′ N, 03° 19.273′ E; 300 m depth, by submersible), *Desmophyllum cristagalli* (April 2007 in Malta 35° 30.506′ N, 14° 06.230′ E; 632 m depth, and at 35° 30.76′ N, 14° 06.42′ E; 585 m depth using an epibenthic sledge), *Madrepora oculata* (July 2006, 42° 23.760′ N, 3° 18.902′ E; 218 m depth by remotely operated vehicle [ROV]). The collection tools used were either an epibenthic sledge on board the RV 'Urania' during the cruise 'MARCOS', or a ROV Phantom HD2 + 2, and the manned submersible JAGO (IFM-GEOMAR) on board the RV 'García del Cid' during the cruises 'Deep Coral I_Coral4' and 'HERMES IV_Coral8.'

Dendrophyllia cornigera forms colonies of 15 cm in height with large polyps of 2 to 4 cm in diameter, and can be found between 200 and 800 m depth, but locally as shallow as 30 m depth (Castric-Fey 1996). Cairns & Zibrowius (1997) considered *Desmophyllum cristagalli* to be a junior synonym of *D. dianthus*. This species forms solitary polyps of 5 to 10 cm in height and 1.5 to 3 cm in diameter, and lives between 100 and 4000 m depth (Risk et al. 2002). The polyps measure ca. 1.5 to 2 cm in height. *Madrepora oculata* forms fragile fan-shaped or cauliflower-like colonies of 30 to 50 cm in height and has small polyps of 3 to 5 mm in diameter. It can be found as shallow as 55 m depth off Brazil and as deep as 1950 m off Iceland (Zibrowius 1980). *Lophelia pertusa* polyps are about 5 to 15 mm in height and ca. 1 cm in diameter, and their colonies grow to a size of more than 130 cm (Gass & Roberts 2006) and form reefs as high as 33 m (Mortensen et al. 2001). This species dwells mostly between 100 and 400 m depth, but has been found at depths of 40 to 3000 m (Zibrowius 1980, Cairns 1994, Freiwald 1998, Fosså et al. 2002).

In the laboratory, corals were maintained for several months to >1 yr in tanks cooled to 12°C, which nearly matches the temperature recorded at the Cap de Creus Canyon (Canals et al. 2006, Palanques et al. 2006). Corals were fed 5 times per week (once daily) with *Artemia salina* nauplii. No damage of the corals from sampling was observed, and the animals continued to survive and grow in the aquaria at the time of writing this manuscript. Four replicated feeding experiments per species (using different colonies) and prey type were conducted in incubation chambers, using a setup that consisted of 3 PVC rectangular chambers (850 ml; dimensions: $200 \times 50 \times 80$ mm) fitted with stirrers with a defined rotational speed. The 3 chambers were in a common water bath to maintain a constant temperature. The system was designed to create a laminar current that circulates around a platform situated in the middle of the chamber (for a detailed description, see

Houlbrèque et al. 2004a). Corals were starved the night prior to the day of the experiment and were placed in the path of the current forcing the prey to repeatedly pass the location until all prey was captured. All experiments were conducted with the minimum flow rate, inducing a current speed of about 1 cm s^{-1}, and was just strong enough to prevent the prey from navigating within the chamber at will, and instead being swept with the current with little control over direction.

The first prey type chosen were adult *Artemia salina* (ca. 8 to 10 mm in length). Both smaller and larger zooplankton organisms were observed during the ROV and JAGO dives (especially Euphausiacea, see Fig. 1), indicating that *A. salina* matches the characteristics of some of the potential prey in the natural habitat. Using live crustacean prey for feeding experiments allows us to consider the efficiency of capturing prey that, once captured, is actively trying to free itself from the tentacles.

One small colony (in the case of *Madrepora oculata* and *Lophelia pertusa*) or solitary polyp (for *Dendrophyllia cornigera* and *Desmophyllum cristagalli*) was placed into each chamber filled with seawater at 12°C. After an acclimation time of 30 min or after polyps opened, 20 adult *Artemia salina* were added to the chamber (23.53 prey items l^{-1}), and their capture by the corals was observed and recorded during an incubation time of 30 min to 2 h (experiments were stopped when the prey quantity in the incubation chamber remained constant, i.e. when the corals stopped feeding). The size of adult *A. salina*, the transparent acrylic material of the chambers, and the efficient capture rate of the corals made direct observation by eye possible. Number of prey ingested was normalized to the number of active polyps. In addition, 4 control experiments per prey type (prey only, without corals) showed that the activity and number of prey remained constant during the incubation.

Live *Artemia salina* nauplii larvae (ca. 0.25 mm in length) were used as alternative prey in a second set of experiments in order to record the capture of smaller zooplankton prey. All experiments started with a prey concentration of 10 to 20 nauplii ml^{-1}. The nauplii were quantified using a dolphus chamber (Riera & Hubas 2003).

Capture rates for both prey sizes were expressed as number of prey polyp^{-1} h^{-1}, and were compared among species using a 1-way analysis of variance (ANOVA; and subsequent Tukey test if appropriate), after confirming that variances were equal (Levene test) and data were normally distributed. Since *Madrepora oculata* rarely ingested this prey type, we failed to obtain a large enough data sample to include in the ANOVA analysis for adult prey. Carbon content was determined using conversion factors by Szyper (1989).

RESULTS AND DISCUSSION

All 4 coral species captured *Artemia salina* nauplii, and 3 of them captured adults as well. Overall, the capture rates per polyp for the 4 species ranged from 5 to 8 adults polyp^{-1} h^{-1} and from 50 to 280 nauplii polyp^{-1} h^{-1} (Table 1). Capture rates for adults were not significantly different among the 4 coral species (ANOVA, $F = 1.72$, p = 0.22), while for nauplii, *Lophelia pertusa* captured significantly more than the other 3 species (ANOVA, $F = 7.7$, p = 0.0033. The polyps were able to capture prey even when expanded only partially. After the experiments, polyps remained saturated and unable to ingest more prey for the next 12 to 24 h. However, the tentacles continued to retain prey, which was either ingested after a period of partial digestion or lost in the current.

Although some studies have demonstrated efficient capture of zooplankton by CWC (e.g. Freiwald 1998), the role of zooplankton in their diet has been questioned in the past. The point raised was that the food spectrum in CWC habitats is possibly lacking zooplankton (Kiriakoulakis et al. 2005), or that the corals were lacking sufficient nematocysts to be able to capture it, as already observed in some tropical shallow water octocoral species (*Briareum asbestinum, Pseudoplexaura porosa, Pseudopterogorgia americana*; Lasker 1981). However, stochiometric studies on CWC have led to the conclusion that zooplankton must be a significant part of their diet (Duineveld et al. 2004, Kiriakoulakis et al. 2005, Dodds et al. in press). We can therefore assume that the CWC studied obtain a part of their diet from capturing zooplankton, as is typical for scleractinian corals in general (Porter 1974, Muscatine & Porter 1977, Sebens 1977, 1987). Mediterranean examples of anthozoans capturing zooplankton include the shallow water octocoral (i.e. gorgonians) or alcyonacean species *Alcyonium siderium, Paramuricea clavata*, and *Leptogorgia sarmentosa* (Coma et al. 1994, Ribes et al. 1998, Rossi et al. 2004). Capture of phytoplankton and bacterioplankton or uptake of dissolved organic matter (DOM) have also been observed among corals and octocorals (Fabricius 1998, Orejas et al. 2001, 2003, Ribes et al. 2003, Picciano & Ferrier-Pagès 2007, Grover et al. 2008), and some Mediterranean species are more or less omnivorous, taking advantage of a wide spectrum of food sources (Ribes et al. 2003, Tsounis et al. 2006). Further research may therefore identify a larger variety of prey types among CWC as well. However, among possible prey types, zooplankton offers the highest energy value, as tropical scleractinian corals have been found to increase their growth by 50 to 75% when a zooplankton diet complements phototrophy (Houlbrèque et al. 2003). Furthermore, when fed with zooplankton, the CWC *Lophelia pertusa* and *Madrepora oculata*

Table 1. Comparison of capture rates of larger plankton, small plankton, and the fine fraction by corals and gorgonians from various latitudes, including the results of the present study. POM: particulate organic matter; POC: particulate organic carbon; CWC: cold water coral

Species	Classification	Capture rate (ind. polyp⁻¹ h⁻¹ ± SD)	Carbon content (µg polyp⁻¹ h⁻¹ ± SD)	Prey	Experimental temperature (°C)	Habitat	Source
Capture of larger plankton							
Madrepora oculata	Scleractinia	2.38 ± 2.31^a	994 ± 996	*Artemia salina*	12	CWC	Present study
Desmophyllum cristagalli	Scleractinia	8.48 ± 2.97	3547 ± 1239	*A. salina*	12	CWC	Present study
Dendrophyllia cornigera	Scleractinia	5.32 ± 1.51	2225 ± 632	*A. salina*	12	CWC	Present study
Lophelia pertusa	Scleractinia	7.82 ± 2.49	3269 ± 1042	*A. salina*	12	CWC	Present study
Plexaura flexuosa	Gorgonian	0.004–0.01	–	Zooplankton (100–700 µm)	25–27	Tropical (asymbiotic)	Ribes et al. (1998)
Pseudoplexaura porosa	Gorgonian	0.004–0.01	–	Zooplankton (100–700 µm)	25–27	Tropical (asymbiotic)	Ribes et al. (1998)
Paramuricea clavata	Gorgonian	1.2–3.3	3.8×10^{-6}–27×10^{-6}	Zooplankton (600–700 µm)	13–22	Temperate	Coma et al. (1994)
Porites lobata	Scleractinia	0.16–5	–	*A. salina*	25–27	Tropical (symbiotic)	Johannes & Tepley (1974)
Oculina arbuscula	Scleractinia	2400–3600	–	*A. salina*	11–20	Temperate	Piniak (2002)
Goniastrea aspera	Scleractinia	0.8	–	Larvae	25–27	Tropical (symbiotic)	Fabricius & Metzner (2004)
Pocillopora damicornis	Scleractinia	4–8	–	*A. salina*	25–27	Tropical (symbiotic)	Clayton & Lasker (1982)
Capture of small plankton							
Madrepora oculata	Scleractinia	47.91 ± 33.29	78.1 ± 54.3	*A. salina* nauplii	12	CWC	Present study
Desmophyllum cristagalli	Scleractinia	93.23 ± 47.65	152 ± 77.7	*A. salina* nauplii	12	CWC	Present study
Dendrophyllia cornigera	Scleractinia	33.29 ± 25.14	189 ± 41	*A. salina* nauplii	12	CWC	Present study
Lophelia pertusa	Scleractinia	283.73 ± 130.09	462 ± 212	*A. salina* nauplii	12	CWC	Present study
Coralium rubrum	Gorgonian	$0.026/0.038 \pm 0.09$	0.13 ± 0.04	Mainly POM & zooplankton	16–18	Temperate	Tsounis et al. (2006)
Leptogorgia sarmentosa	Gorgonian	0.16 ± 0.02	0.019 ± 0.002	Zooplankton	17–18	Temperate	Rossi et al. (2004)
Madracis mirabilis	Scleractinia	6–15	–	Natural plankton	25–27	Tropical (symbiotic)	Sebens et al. (1996)
Montastrea cavernosa	Scleractinia	30	–	Natural plankton	25–27	Tropical (symbiotic)	Sebens et al. (1996)
Pocillopora damicornis	Scleractinia	0.7–5	–	Natural plankton	25–27	Tropical (symbiotic)	Palardy et al. (2006)
Pavona gigantea	Scleractinia	2–18	–	Natural plankton	25–27	Tropical (symbiotic)	Palardy et al. (2006)
Pavona clavus	Scleractinia	3–12	–	Natural plankton	25–27	Tropical (symbiotic)	Palardy et al. (2006)
Montastrea cavernosa	Scleractinia	0.08–6	–	Natural plankton	25–27	Tropical (symbiotic)	Porter (1974)
Capture of fine fraction							
Dendronephthya hemprichi	Soft coral	–	$5.1 \times 10^{-6} \pm 0.9 \times 10^{-6}$	Phytoplankton	25–27	Tropical (asymbiotic)	Fabricius (1998)
Paramuricea clavata	Gorgonian	–	19.1	Live POC	16–18	Temperate	Ribes et al. (1999)
Paramuricea clavata	Gorgonian	–	2.2×10^{-6}	Detrital POC	16–18	Temperate	Ribes et al. (1999)
Leptogorgia sarmentosa	Gorgonian	213 ± 68	$6.8 \times 10^{-2} \pm 3.2 \times 10^{-2}$	Nanoeukaryotes, phytoplankton, ciliates, detrital POC	16–18	Temperate	Ribes et al. (2003)
Primnoisis antarctica	Gorgonian	–	4.63×10^{-4}	Diatoms (77%), dinoflagellates (20%)	0	Antarctic CWC	Orejas et al. (2003)
Primnoella sp.	Gorgonian	–	5.58×10^{-3}	Dinoflagellates (92%), diatoms	0	Antarctic CWC	Orejas et al. (2003)

[a]Few data points, as prey size were too large and capture usually failed

showed growth rates in the same range as some tropical corals (Orejas et al. 2008). Thus when zooplankton is available, it likely represents an important part of the diet of corals.

The chosen prey type in this study is at best only representative for a small part of their food spectrum, but these experiments do demonstrate the feeding efficiency of the 4 studied coral species for this kind of prey. In fact, the results reveal some differences in the feeding capacities among the corals. In this study, *Madrepora oculata* usually failed to capture adult *Artemia salina* (despite some data points that are included in the table, but were not sufficient to meet ANOVA requirements). Although we did not focus on determining the cause for these differences, it is known that species differing in colony size, colony structure, polyp size, tentacle size, and nematocyst density on the tentacles capture a different size spectrum of prey (Lasker 1981, Sebens & Koehl 1984, Palardy et al. 2005). The polyps of *Dendrophyllia cornigera* and *Desmophyllum cristagalli* are much larger (20 to 40 mm in diameter) than those of *Lophelia pertusa* and *M. oculata* (3 to 10 mm in diameter), and thus a much higher capture rate would be expected in the former species. However, our results showed that the *D. cornigera* and *D. cristagalli* colonies did not capture significantly more prey than *L. pertusa*, which proved to be a relatively voracious grazer despite its smaller polyp size (Fig. 2). The potential prey size spectrum that this species can efficiently capture is remarkably ample, as aquarium and *in situ* observations have provided evidence that *L. pertusa* is able to selectively capture live zooplankton up to 2 cm in size (Mortensen 2001, Freiwald 2002). The high capture rate of *A. salina* nauplii may indicate that this prey lies within the optimal prey size range for the 4 studied CWC species, but further research is needed to confirm this observation. Although the 4 species captured nauplii at a higher rate than adults, capture of nauplii results in lower energetic input, since the energetic value of adult *Artemia* sp. (see Table 1) is much higher than that of nauplii. However, juvenile *Artemia* sp. have a much lower energetic value (Szyper 1989) so that their capture may result in a lower energy input as in the case of nauplii larvae.

In comparison to other corals, even tropical zooxanthellate species such as *Stylophora pistillata* (Ferrier-Pagès et al. 2003), it appears that the capture rates and energy input of the studied CWC species are on a comparable level (Table 1). Some studies on other corals used a similar experimental set up, so that the comparison of results should be valid (Ribes et al. 1998, Orejas et al. 2003, Houlbréque et al. 2004a). However, some tropical corals might have low capture rates due to complementing their energy demand with zooxanthel-
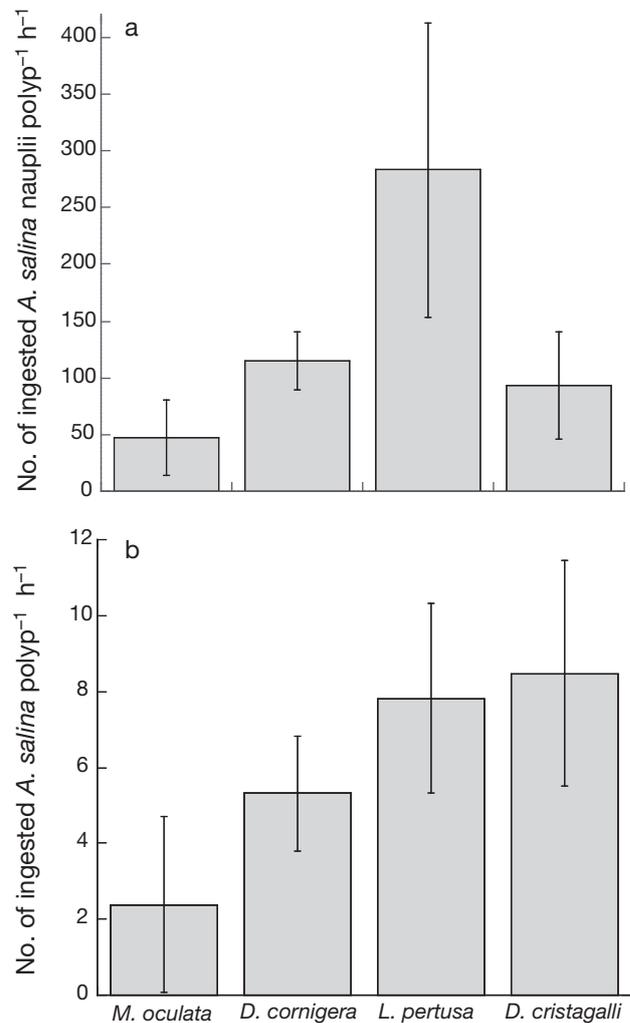

Fig. 2. *Madrepora oculata, Dendrophyllia cornigera, Lophelia pertusa,* and *Desmophyllum cristagalli*. Capture rates (expressed as average ± SD) of *Artemia salina* (a) adults and (b) nauplii larvae

lae. In contrast to tropical corals, CWC dwell in a habitat with low temperature, which implies lower energy expenditure. Thus CWC may be able to exploit a large amount of energy from potentially short zooplankton pulses, and possibly survive even if such pulses are sparse.

In general, feeding rates measured with incubation chamber experiments are difficult to extrapolate to the natural environment, since the natural habitat has extremely varying conditions. *In situ* capture rates might vary according to the current speed and prey availability and may be in the form of pulses (Omori & Hamner 1982, LaBarbera 1984, Eckman & Duggins 1993, Kim & Lasker 1997). Caution must therefore be used when extrapolating capture rates obtained in the laboratory to *in situ* conditions.

Future studies may determine the grazing impact of these coral species on the ecosystem by utilizing a biometrical characterization of the colony morphology, as e.g. *Madrepora oculata* colonies have far more polyps than *Dendrophyllia cornigera* and *Desmophyllum cristagalli* and will therefore capture more prey despite a lower capture rate per polyp. Future research should also include studies on population structure, digestion times, and activity rhythms of CWC, as well as studies on the temporal and spatial distribution and dynamics of zooplankton in the near bottom layer. These studies will ultimately improve our understanding of biogeochemical fluxes in deep ocean habitats, and the ecology of CWC.

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