



# Food Preferences of Mediterranean Cold-Water Corals in Captivity

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Cold-water coral (CWC) systems are hotspots of biodiversity that need protection from the increasing human impacts and global climate change. The restoration of degraded cold-water coral reefs may be conducted through transplantation of nubbins. To do so, we need to set up the optimal conditions for CWCs livelihood in an aquarium setting. Here we investigated the food selection of three cold-water coral species inhabiting the NE Atlantic Ocean and the Mediterranean Sea to identify the optimal feeding conditions to rear corals, by means of stable isotope analysis ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) and of prey-capture rates. Colonies of *Desmophyllum pertusum*, *Madrepora oculata* and *Dendrophyllia cornigera* were collected in the Mediterranean Sea and nourished in mesocosms with a) nauplii of *Artemia salina*, b) the green algae *Tetraselmis subcordiformis*, c) two rotifer species (*Brachionus plicatilis* and *B. rotundiformis*) and d) mysids of the species *Mysis relicta*. Prey-capture rates coupled with isotope analysis revealed that *M. relicta* was the preferred food source even if it was provided as a frozen item, followed by the live-items *A. salina* and *Brachionus* spp. Isotopic analyses allowed to determine that Particulate Organic Matter (POM) appears to contribute to a large portion of the isotopic composition of the coral tissue and also suggested that *M. oculata* has the most opportunistic behaviour among the three target coral species. This study confirms that it is possible to optimize CWCs livelihood in aquaria choosing the right food sources during their maintenance, also in preparation to their transplant in degraded habitats during future projects of active restoration.

**Keywords:** cold-water corals, *Desmophyllum pertusum*, *Madrepora oculata*, *Dendrophyllia cornigera*, food selection, stable isotopes, restoration, Mediterranean Sea

## 1 INTRODUCTION

Cold-water corals (CWCs) are important habitat-forming species including azooxanthellate stony corals (Scleractinia), gorgonians (Alcyonacea), black corals (Antipatharia) and hydrocorals (Stylasteridae) (Roberts et al., 2006). CWCs and their habitats are receiving great interest from the scientific community due to their high ecological value (Roberts et al., 2009). Cold-water reefs formed by stony corals are complex three-dimensional structures and are biodiversity hotspots (Henry and Roberts, 2007; Hovland, 2008; Bongiorno et al., 2010; Mastrototaro et al., 2010; Rueda et al., 2019) acting as nurseries, refugia or feeding grounds for several species of fishes and invertebrates (Baillon et al., 2012; D'Onghia, 2019).

CWCs are threatened by several anthropogenic activities (D'Onghia et al., 2016; Ragnarsson et al., 2016; Montseny et al., 2021). Among them, deep-sea fisheries directly affect CWC reefs (D'Onghia, 2019), up to an estimated 95–98% of the total coral cover (Gianni, 2004). Oil and gas exploitation is extending at deeper depths, increasing the risks of oil-spill accidents or dispersal near CWC reefs (Cordes et al., 2016). Also, deep-sea mining might affect CWC reefs that are often located near sites of exploitation (Roberts and Cairns, 2014; Ragnarsson et al., 2016). In addition, global climate change represents a serious concern for CWCs as the reduction of pH determines a decrease of the depth of aragonite saturation horizon (Ragnarsson et al., 2016; Sweetman et al., 2017) and increasing rates of skeletal dissolution (Gómez et al., 2018). Acidification and higher water temperatures are proved to affect cold-water corals also by increasing their vulnerability to other environmental stressors like chemical pollution (Weinnig et al., 2020). Projections indicate that 70% of the actual locations of CWC ecosystems could become under-saturated by 2099 (Guinotte et al., 2006).

Ecosystem restoration is a key action of several frameworks and conventions both at European and global level. Restoration of damaged CWCs ecosystems will be increasingly required in the future, even because sequestration of carbon dioxide from seawater by CWCs (Turley et al., 2007) constitutes an essential regulating service and, because of this, the deep sea has been proposed as storage environment for the surplus CO<sub>2</sub> produced by humans with the use of fossil fuels (Davies et al., 2007).

Considering that the research field on ecological restoration of deep-sea ecosystems is still in its infancy (Da Ros et al., 2019), only few studies focus on CWCs active restoration actions, as reported in the literature (Montseny et al., 2021). The transplantation of nubbins taken from healthy colonies or reared in aquaria into degraded coral grounds is the preferred restoration action (Da Ros et al., 2019 and references therein). Pilot experiments on transplantation of nubbins of *Desmophyllum pertusum* were carried out in the Gulf of Mexico, in the North Sea and off Central California, with encouraging results of high survival rates for *D. pertusum* (Brooke and Young, 2009; Dahl, 2013; Boch et al., 2019). Recently, in the Mediterranean Sea and in the Atlantic (Azores Archipelago), several CWCs, including fan corals, were transplanted to evaluate their survival rate (Linares et al., 2020).

The success of maintenance of CWCs in aquaria can be affected by variations of physical parameters (mainly flow velocities and temperature) that can also influence the feeding behaviour of CWCs like widely demonstrated in literature (Purser et al., 2010; Gori et al., 2015; Orejas et al., 2016).

*Artemia salina* is often used for keeping CWCs in aquaria and for conducting feeding experiments because it has the same size of target copepods (Orejas et al., 2019 and references therein). Usually, rotifers in aquaria are provided as feeding supplementary to corals characterised by very small polyp size, like black corals (e.g., *Bathypathes* sp. and *Leiopathes glaberrima*) or gorgonians (es *Dentomuricea meteor*) (Orejas et al., 2019). In captivity, nauplii of *A. salina* (Linnaeus, 1758) and algae are routinely used to also feed *D. pertusum* (Orejas et al., 2019), while *Mysis* sp. (Latreille, 1802) and adults of *A. salina* are used to feed *D. cornigera* (Gori et al., 2015; Orejas et al., 2019).

In the Mediterranean Sea, the most common reef-building CWCs are the 'white corals' *Desmophyllum pertusum* (Linnaeus 1758), formerly known as *Lophelia pertusa* (Addamo et al., 2016), and *Madrepora oculata* (Linnaeus, 1758). These two taxa often co-occur and engineer the CWC-grounds with maximum areal occupancy in the coral provinces identified in the central and western Mediterranean Sea, between ca. 200–800 m (Fanelli et al., 2017; Taviani et al., 2017; Chimienti et al., 2019; Taviani et al., 2019) at a temperature comprised between 11 and 13.9°C (Naumann et al., 2014). *In-situ* observations carried out through ROVs along Bari canyon and on the Apulian Plateau showed that *M. oculata* is the dominant species of CWCs in the Central Mediterranean Sea (Freiwald et al., 2009), probably due to the environmental conditions that in this basin are closed to the ecological limits of this species (Davies et al., 2008). The "yellow coral" *Dendrophyllia cornigera* (Lamarck, 1816) forms colonies from the mesophotic zone down to bathyal depths, where it often mingles with white corals (Castellan et al., 2019). In the Mediterranean Sea, this eurybathic species lives in a temperature range between 7 and 16°C (Castellan et al., 2019).

Here we investigated the feeding preferences of *D. pertusum*, *M. oculata* and *D. cornigera* to establish the best conditions to keep them in captivity and for maintaining them on-board during the oceanographic campaigns. Four food sources were chosen to feed the corals and establish their food preferences: 1) nauplii of *A. salina*, 2) the green algae *Tetraselmis subcordiformis*, (Wille) Butcher 1959, 3) two species of rotifers (*Brachionus plicatilis*, Müller, 1786, and *B. rotundiformis*, Tschugunoff, 1921) and 4) the crustacean mysid *M. relicta* (Lovén, 1862).

The main goal of this study is to determine the best conditions for successfully and effectively keeping CWCs alive in aquaria, in face of increasing request of such kind of knowledge for restoration of marine degraded habitats as promoted by the UN Decade on Ecosystem Restoration (UNGA, 2019) at global level and by the EU 2030 Biodiversity Strategy (EC, 2020) at European level. Specific aims of this study are: 1) to determine the isotopic signatures of the exposed specimens to discriminate between ingested vs. assimilated food items and their resource partitioning (i.e., which of the captured preys were preferentially assimilated by the different species) and 2) to increase our understanding on the feeding ecology of CWCs occurring in the Mediterranean Sea.

## 2 MATERIALS AND METHODS

Three species of cold-water corals were sampled using a ROV (Remotely Operated Vehicle), during two oceanographic campaigns conducted in 2016 in the Mediterranean Sea on-board of RV *Minerva Uno*. In order to reflect the cold-water coral community structure of the Central Mediterranean Sea, one live colony of *D. pertusum* (made up of 280 polyps) and 4 colonies of *M. oculata* (with a total of 1501 polyps) were collected during the SIRIAD16 oceanographic campaign at depth of 244 and 400 m, respectively, in the south-western Adriatic Sea (Figure 1). One colony of *D. cornigera* (made up of 9 polyps) was collected at 139 m depth, during the RISD\_16 campaign, in the northern

Ionian Sea (**Figure 1**). Corals were kept alive inside 20 L PVC darkened aquaria filled with bottom seawater (previously filtered with a 20  $\mu\text{m}$ -mesh) collected simultaneously to corals, without feeding them due to the logistical limitations on board, according to literature (Orejas et al., 2019).

Once in the laboratory, the colonies were kept in different aquaria (one tank for each species, a 30 L tank for *D. cornigera*, two 50 L tanks for *D. pertusum* and *M. oculata*, with the 4 colonies of *M. oculata* kept together in the same aquaria to better simulate the community structure) filled with bottom seawater (previously filtered with a 20  $\mu\text{m}$ -mesh). Before choosing how to divide the colonies and the volumes of the tanks to use, we checked that the estimated total dry weights of the collected species were similar, according to dry weights values reported in Maier et al., 2012 for *D. pertusum* and *M. oculata* and in Gori et al., 2014 for *D. cornigera*.

Corals were maintained in the dark and at a temperature of  $13 \pm 0.5^\circ\text{C}$ . Although corals were collected in different sites, the *in-situ* temperature was similar, (**Table S1**), thus we set the temperature at ca.  $13^\circ\text{C}$  for all the three species as this is the mean temperature of the deep waters in the Western and Central Mediterranean Sea (Danovaro et al., 2010), with the maximum recorded temperature for the occurrence of *D. pertusum* at  $13.8^\circ\text{C}$  in the Ionian Sea (Freiwald et al., 2004). Temperature was maintained constant through a common water bath and a refrigerator (TECO SeaChill Chiller TR5). Seawater was sampled in the central Adriatic Sea and filtered with a 20  $\mu\text{m}$ -mesh prior to gradually mix it with the bottom seawater of the aquaria (final salinity  $37 \pm 0.2$  PSU). Subsequently,  $\sim 60\%$  of the seawater in the tanks was exchanged every 10 days. Every day, the bottom of the tank was cleaned with an aquarium siphon to ensure build-up of detritus to be minimal.

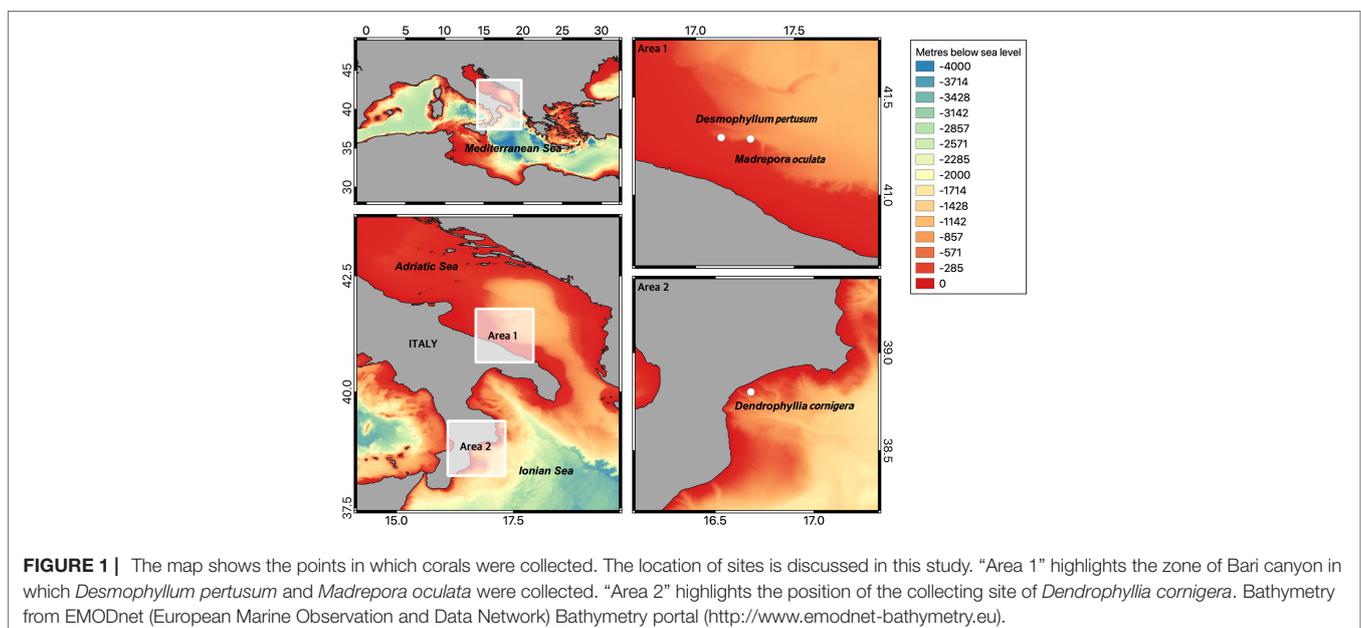
Due to the difficulties in replicating the natural complexity of the environments from which the corals were collected in

laboratory settings, and differently from previous studies that focused on the effects of current velocities on their feeding capacity, here we maintained a constant water recirculation using submersible pumps with a flow rate of  $\sim 2000$  L  $\text{h}^{-1}$  (Orejas et al., 2019). The flow velocity was maintained in a range of 5–10  $\text{cm s}^{-1}$  to better simulate the natural conditions of collection areas (Turchetto et al., 2007; Langone et al., 2016) with peaks of  $\sim 20$   $\text{cm s}^{-1}$  in the tank of *D. cornigera* (Davies et al., 2009). Pumps water-outlets were coated with a 20  $\mu\text{m}$ -NITEX nylon mesh in order to avoid harming of prey items.

An air stone oxygenated the seawater and was placed at the top of the aquaria preventing any influence on polyps' activity. The oxygen concentration was maintained at *in-situ* conditions ( $5.2 \pm 0.2$  mL  $\text{L}^{-1}$ ) (Davies et al., 2008). We started the experiment when the colonies completely extended their polyps without showing stress signals (e.g., mucus production) (Murray et al., 2019). This acclimation period lasted 4 weeks for *D. pertusum* and *M. oculata* (Chapron et al., 2018) and 2 weeks for *D. cornigera*. Since the filtered seawater still contained sufficient organic particles, no extra food had to be provided during the acclimation period (van Oevelen et al., 2018). Food was provided when at least the 90% of the polyps of the colonies were open.

## 2.1 Behavioural Observations

Corals' behaviour and their response to presence of food or light were observed and these qualitative data were collected to gather essential information at best maintenance in aquaria. Twice a day, at 9 a.m. and at 6 p.m., polyps' activity and tissue conditions were monitored to exclude stress signs like tissue sloughing and loss, and extensive mucus production (Orejas et al., 2019). During the first twenty minutes from the provisioning of food, corals' reaction to the presence of food items was observed. During all the monitoring, we used a weak lighting screened with red filters to reduce possible impacts by the necessary light exposure (Orejas et al., 2019).



## 2.2 Set Up of the Feeding Experiments

*Artemia*'s dry cysts (1 g) were placed inside a conical *Artemia* hatchery filled with 2 L of pre-filtered 0.7  $\mu\text{m}$  seawater (filtered using Whatman GF/F filters) with intensive light. After 24 hours, nauplii were hatched and used for the experiment. The green algae *T. subcordiformis* was cultured in 500 mL Erlenmeyer flasks filled with sterile F/2 medium (Guillard, 1975). The cultures were maintained at 21°C, lightened by a continuous light with a photon flux density of 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (400-700 nm). *B. plicatilis* and *B. rotundiformis* were cultured at 21°C in a tank with mechanical aeration filled with pre-filtered 0.7  $\mu\text{m}$  seawater at a salinity of 33 (Yufera et al., 1997). Rotifers were fed with baker's yeast (Orejas et al., 2019). These food sources were selected for the highly standardised rearing protocols and the variety of the composition, which can simulate a wide range of potential coral preys (Orejas et al., 2019). On the contrary, mysids are not easy to rear due to the common cannibalism of the adults towards juveniles (Mauchline, 1980). For this reason, *M. relicta* was supplied from frozen stocks and kept in suspension using an intense water recirculation (Orejas et al., 2019).

For each species, each food source was provided in the same total amount (total biomass expressed as  $\mu\text{g}$  of C). *D. pertusum* and *M. oculata* (for both species, around 75  $\mu\text{gC L}^{-1}$  from each food source, a biomass determined considering the amount of nauplii of *A. salina* provided by Larsson et al., 2013) were fed twice a week, while food items were provided to *D. cornigera* three times a week (around 250  $\mu\text{gC L}^{-1}$  for each food source, a biomass determined considering the amount of nauplii of *A. salina* provided by Gori et al., 2015). Food sources' biomass was determined using literature data (*T. subcordiformis*) and bio-volumetric measurements (zooplankton). Body volumes of *M. relicta*, *A. salina*, *Brachionus* spp. were determined with a stereomicroscope (LEICA WILD L3B) with micrometric grids. The biovolume and the biomass of rotifers was calculated accordingly to Gradinger et al. (1999). For crustaceans, the biovolume was calculated from the body width (W) and length (L) (ten specimens for each food source) using the formula  $V=L \times W^2 \times C$ , where C is an a-dimensional factor (Gambi et al., 2019). We assumed an average density of 1.13  $\text{g cm}^{-3}$  to calculate the wet biomass and then the dry weight ( $\mu\text{g}$  dry weight:  $\mu\text{g}$  wet weight = 0.25) (Wieser, 2007). The carbon content was considered as the 40% of the dry weight (Higgins and Thiel, 1988).

## 2.3 Stable Isotope Analysis

Stable-nitrogen ( $\delta^{15}\text{N}$ ) and stable-carbon ( $\delta^{13}\text{C}$ ) isotope ratios were determined in the three species. These values can provide useful information in dietary studies and are commonly applied to analyse marine food webs (DeNiro and Epstein, 1978; Post, 2002; Fry, 2006; Layman et al., 2012) providing an indication of the origin and transformations of organic matter (i.e., food assimilated) (Peterson and Fry, 1987; Layman et al., 2007; Newsome et al., 2007). The  $\delta^{15}\text{N}$  in tissues of consumers are typically greater by 2–3‰ relative to their prey so that  $\delta^{15}\text{N}$  data can be used to estimate the trophic levels of organisms (Owens, 1988).  $\delta^{13}\text{C}$  may act as a useful indicator of primary organic carbon sources of an animal's diet, as tissues tend to be rather

weakly enriched in  $^{13}\text{C}$  at progressively higher trophic levels (less than 1‰; DeNiro and Epstein, 1978). Stable Isotope Analysis (SIA) results allowed also to better understand the trophic ecology of the investigated species in the Central Mediterranean Sea.

Once arrived at the laboratory, one third of the sampled colonies was immediately frozen at  $-20^\circ\text{C}$  ( $T_0$ ). SIA was conducted only on the soft bodies of the animals to avoid the interference of the C signal provided by the analysis of the entire calyx (Sherwood et al., 2008). Samples from the different cultures of the food sources were collected and frozen. At the end of the experiment, that lasted 30 days ( $T_f$ ), samples of each of the coral species (at least  $n=5$  samples with at least 3 polyps for each species) were collected and immediately frozen. Samples were then dried for 24 h at  $60^\circ\text{C}$  and ground to a fine powder with a mortar and a pestle (Fanelli et al., 2011). Except for algae and rotifers, subsamples were acidified adding drop by drop HCl 1M (Sigma-Aldrich, CAS Number 7647-01-0) to remove inorganic carbonates. Cessation of bubbling was used as signal of completion of the reaction. These subsamples were dried again at  $60^\circ\text{C}$  for 24 h (Jacob et al., 2005). Some samples were acidified (and dried) once again until complete removal of inorganic carbonates. All the samples were weighed (ca. 1 mg of dry weight) in tin capsules (Elemental Microanalysis Tin Capsules Pressed, Standard Weight 5 x 3.5 mm). Stable isotope measurements were carried out by an elemental analyser coupled to an isotope ratio mass spectrometer (ThermoFisher Flash EA 1112 elemental analyzer coupled to a Thermo Electron Delta Plus XP isotope ratio mass spectrometer, IRMS) according to standard protocols (Fanelli et al., 2009; Fanelli et al., 2011; Rumolo et al., 2016). Briefly, the samples were run against blank cups and known urea standards. Three capsules of urea were analysed at the beginning of each sequence and one every six samples as a quality control measure and to compensate for potential machine drift. Experimental precision (based on the standard deviation of replicates of the internal standard) was  $<0.1$  ‰ for  $\delta^{15}\text{N}$  and  $<0.2$  ‰ for  $\delta^{13}\text{C}$ . The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric  $\text{N}_2$  standards, respectively, according to the following formula:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3$$

where  $R=^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . At least three replicates for samples were analysed.

## 2.4 Prey-Capture Rate Experiments

The prey-capture rate was evaluated for each of the three species. For this experiment, we followed the protocol reported in Tsounis et al. (2010). Fresh living zooplankton and phytoplankton were mixed and added in the aquaria, twice a week (for 30 days) for *D. pertusum* and *M. oculata*, and three times a week for *D. cornigera*. Frozen individuals of *M. relicta* were added at the same time. Seawater in the aquaria was gently mixed by a continuous slight aeration (Piccinetti et al., 2016) and by the submersible recirculation pumps ( $\sim 2000 \text{ L h}^{-1}$ ). Seawater

was vigorously mixed, and samples (100 mL for 3 replicates) were taken from each tank after a couple of seconds and after 5 hours (Orejas et al., 2016). Samples were preserved with 4% formaldehyde (Sigma-Aldrich, CAS Number 50-00-0) (Orejas et al., 2016) and, after 24 hours, individuals of *A. salina* and *Brachionus* spp. were counted using a Dolphus curve (Tsounis et al., 2010) and a stereomicroscope (LEICA WILD L3B). For counting *T. subcordiformis* cells, replicates of 60 mL of seawater were collected at the same time from each tank and preserved for 24 hours with 2% formaldehyde. Replicated subsamples of 1 mL of seawater were observed using a Sedgewick-rafter counting chamber and algae cells were counted under a microscope (Orejas et al., 2016). Averaged prey-capture rate was normalized to the number of polyps present in each mesocosm to determine the number of nauplii captured by each polyp at each hour. Each time after feeding, the uneaten food was removed (Orejas et al., 2019). Control experiments were run under the same conditions but without corals to determine the percentage loss of prey items in each different aquarium and to correct the values of the determined prey-capture rates.

## 2.5 Data Treatment

Statistical analyses were carried out using R (4.0.5 version R Development Core Team, 2021). After testing the homogeneity of variances using Bartlett's test, one-way analysis of variance (ANOVA) was performed with the R function "aov" to test for differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  contents of each species between the two sampling periods. same approach was used to test differences among the assumption of C from the different food sources by the three coral species. When significant differences were encountered with ANOVA, a Tukey's *post-hoc* comparison test was performed with the R function "TukeyHSD" to ascertain differences among the contributions of C provided by the different food sources. For all the analyses,  $p < 0.05$  was considered the significant threshold.

To provide an estimate of the relative contributions of the different sources to the isotopic content of the samples, the package Stable Isotope Mixing Models in R (simmr) was used (Parnell, 2021). Simmr is designed as an upgrade of the package SIAR (Stable Isotope Analysis in R) (Parnell and Jackson, 2013) and it is designed to solve mixing equations for stable isotopic data within a Bayesian framework. The standard deviation depends on the intraspecific variability among the individuals and on the uncertainty of fractionation corrections. In this study, we used for  $^{13}\text{C}$  the Trophic Enrichment Factor (TEF) of  $1.0 \pm 0.1$  ‰ (Ferrier-Pagès et al., 2011) and for  $^{15}\text{N}$  the TEF of several consumers' diets that is  $2.5 \pm 0.1$  ‰ (Carlier et al., 2009).

Before running the model, the isotopic values of the sources and of the three species of corals were plotted together, applying the correct TEFs to determine the mixing polygon (Smith et al., 2013; Phillips et al., 2014) of the CWCs community. We excluded *T. subcordiformis* as food source due to its very high  $\delta^{15}\text{N}$  isotope value which remains far outside the mixing polygon (Jackson et al., 2011; Phillips et al., 2014). The corals isotopic values did not fall completely within the range of the food source isotopic values, so we decided to use data from the literature to better

construct the mixing polygon and to define the sources which to run the model with (Phillips et al., 2014) (**Figure S1**). One of the potential food sources for CWCs is the particulate organic matter (POM) contained in the seawater (Mueller et al., 2014). In this study, we used two different POM values as inputs in simmr, based on the hypothesis that CWCs can be influenced by both the Bari Canyon POM during the collection, transportation, and the beginning of the experiment, and by the Northern Adriatic Sea POM for the other part of the experiment, as we used Adriatic seawater for maintaining corals in our laboratory. The values of the isotopic content of POM of the Bari Canyon ( $\delta^{15}\text{N} = -2.6$  ‰ and  $\delta^{13}\text{C} = -21.7$  ‰) and POM of the Adriatic Sea (summer period,  $\delta^{15}\text{N} = 7$  ‰ and  $\delta^{13}\text{C} = -22$  ‰) were taken from the literature (respectively from Carlier et al., 2009 and from Faganeli et al., 2009).

To examine the trophic targets of each species, SIBER package (Stable Isotope Bayesian Ellipses in R) was used (Jackson et al., 2011). SIBER allowed to determine the trophic preference of the three species. Layman metrics, which provide quantitative measures of the trophic structure of a community, were also calculated in SIBER, specifically:  $\delta^{13}\text{C}$  range (CR),  $\delta^{15}\text{N}$  range (NR), total area of the convex hull (TA), mean distance to centroid (CD) (Layman et al., 2007). CR provides information on the diversity of the resources at the base of the trophic web with higher values that indicate multiple basal carbon sources; NR gives information on the trophic length of the community and CD estimates trophic diversity within a food web and is a function of the degree of species spacing lower numbers indicate that distinct taxa are exhibiting similar ecological functions (Jackson et al., 2011). TA gives an indication of the variety of food items but is highly sensitive to sample size (Layman et al., 2007). Simmr and SIBER were used also to calculate the corrected Standard Ellipse Areas ( $\text{SEA}_C$ ) that is the sample-size corrected population isotopic targets (Jackson et al., 2011) allowing the comparison between the preferences of the three species (classified as groups of the same community). It contains approximately 40% of the data within a set of bivariate data and thus represents the core area for a population or community (Layman et al., 2007; Jackson et al., 2011). Overlap of isotopic data suggests, at least in part, an overlap of resource usage by the groups (Layman et al., 2007; Jackson et al., 2011). The percent overlap is given by the percent of the overlapping area over the total area covered by the two ellipses (Krumsick and Fisher, 2019). All the analyses were carried out using R.

## 3 RESULTS

### 3.1 Behavioural Observations

Even if this experiment was not set to study corals polyp activity and behaviour, these observations were reported to provide additional information on corals' feeding behaviour. Among the three species, *D. cornigera* was the most reactive one, with all the polyps opened after 2 weeks of acclimation. It reacted to each food provisioning by moving tentacles to capture preys. Also *M. oculata* expanded the polyps' tentacles when it detected the presence of food items, while *D. pertusum* seemed to be the

most light-sensible species, withdrawing polyps and producing mucus even when exposed to a weak light (used during sampling operations). At the end of the experiment, the corals did not display signals of stress.

### 3.2 Results of Stable Isotope Analysis

The isotopic content of the food items provided to the three coral species, varied from 6.41 ‰ (in *M. relicta*) to 14.58 ‰ (in *T. subcordiformis*) for  $\delta^{15}\text{N}$ , and from  $-20.5$  ‰ (in *M. relicta*) to  $-14.5$  ‰ (in *Brachionus* spp.) for  $\delta^{13}\text{C}$  (Table 1).

At the end of the experiment ( $T_1$ , after 30 days from the beginning of the feeding experiment)  $^{15}\text{N}$  values were more enriched in all the species. *D. pertusum* showed a significant increase in the  $\delta^{15}\text{N}$  value of 2.9 ‰ (from  $3.4 \pm 0.4$  to  $6.3 \pm 0.5$ ,  $p < 0.001$ ). In *M. oculata* the increase was of 0.8 ‰ (from  $3.3 \pm 0.9$  to  $4.1 \pm 1.8$ ,  $p > 0.05$ , not significant) and in *D. cornigera* the significant increment was of 1.2 ‰ (from  $4.8 \pm 0.6$  to  $6.0 \pm 0.6$ ,  $p < 0.05$ ) (Figure 2A and Table 2). The isotopic signals in *D. pertusum* and *M. oculata* were  $^{13}\text{C}$ -depleted (respectively from  $-19.9 \pm 0.3$  ‰ to  $-20.7 \pm 0.8$  ‰ and from  $-19.5 \pm 1.9$  ‰ to  $-20 \pm 1.7$  ‰,  $p > 0.05$ , not significant) but for *D. cornigera* the values of  $\delta^{13}\text{C}$  showed an increase (from  $-21 \pm 0.5$  ‰ to  $-20.4 \pm 1.7$  ‰,  $p > 0.05$ , not significant) (Figure 2B and Table 2).

Simmr provided the proportional contribution of each food source to the diet of the three CWC species (Figure 3). At  $T_0$ , the

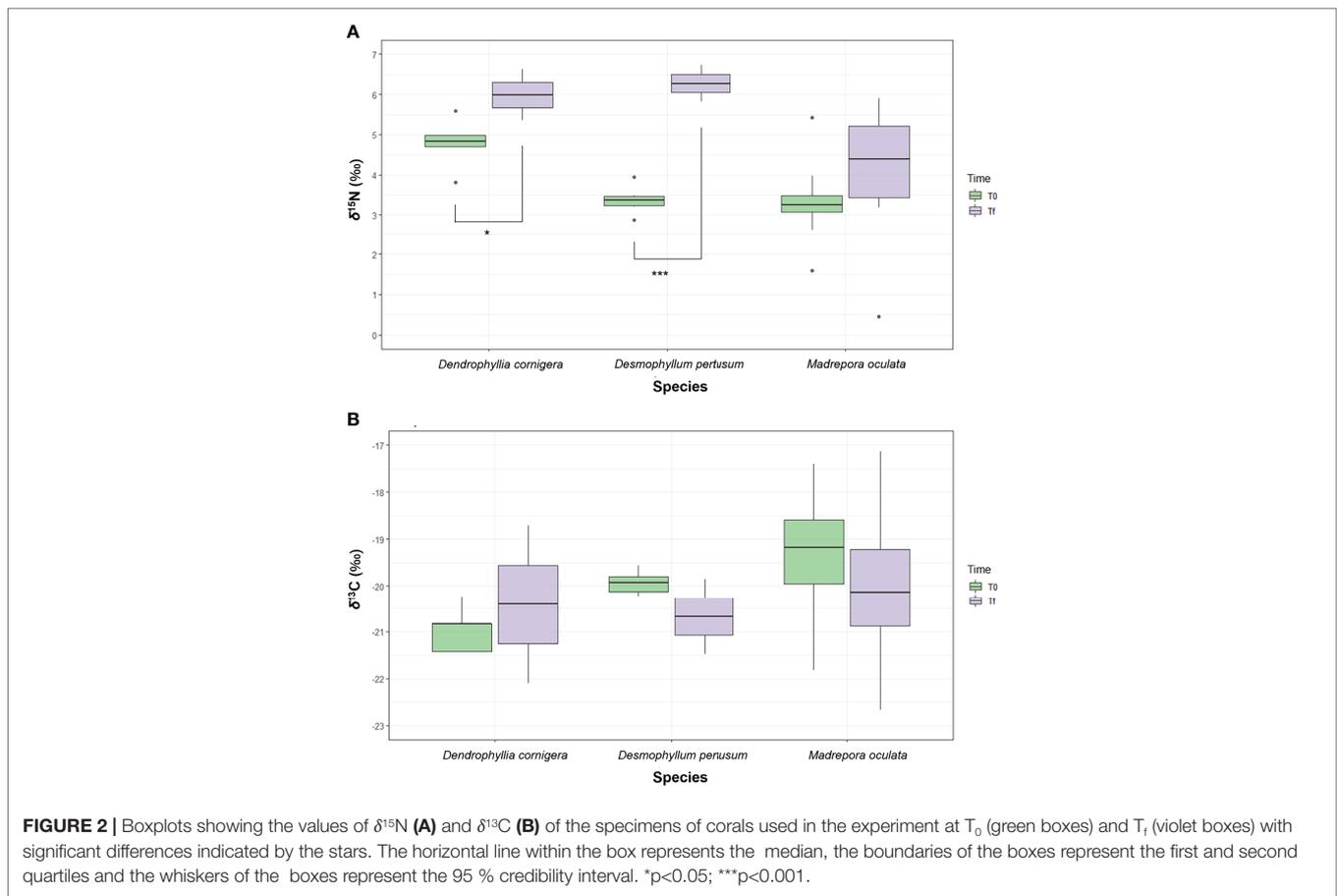
**TABLE 1** | Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of the food sources provided to the corals.

Food sources	$\delta^{15}\text{N}$ (‰)	SD	$\delta^{13}\text{C}$ (‰)	SD
<i>Mysis relicta</i>	6.41	<0.05	-20.5	0.1
<i>Artemia salina</i>	11.97	0.1	-19.62	<0.05
<i>Brachionus</i> spp.	9.03	0.1	-14.5	0.2
<i>Tetraselmis subcordiformis</i>	14.58	<0.05	-14.76	<0.05

SD, standard deviation.

major contribution to the isotopic composition of the three species was given by the POM of Bari canyon (means were of 64.9% in *D. pertusum*, 65.7% in *M. oculata*, 48.3% in *D. cornigera*) (Figure 3). After 30 days, the proportion of the contribution of POM of Bari canyon to CWC's diet decreased (30.6% in *D. pertusum*, 54.1% in *M. oculata*, 32.8% in *D. cornigera*), while that of North Adriatic Sea POM increased ( $64.9 \pm 0.04\%$  in *D. pertusum*, 12.6% in *M. oculata*, 48.3% in *D. cornigera*) together with the contribution of *M. relicta* (19% in *D. pertusum*, 12.6% in *M. oculata*, 18.6% in *D. cornigera*) (Figure 3), *A. salina* (12.1% in *D. pertusum*, 9% in *M. oculata*, 12.6% in *D. cornigera*) and *Brachionus* spp (9.3% in *D. pertusum*, 7.6% in *M. oculata*, 10.7% in *D. cornigera*). The simmr output is presented as the full distribution of the prior and posterior probability density function (Figure S2).

Standard ellipses showed that *M. oculata* has the widest isotopic variability and *D. cornigera* the smallest one (Figure 4). Additionally, Layman metrics (Table 3) indicated that *D.*



**TABLE 2** | Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of the corals at the beginning ( $T_0$ ) and at the end ( $T_f$ ) of the experiment.

Time	Species	$\delta^{15}\text{N}$ (‰)	SD	$\delta^{13}\text{C}$ (‰)	SD
$T_0$	<i>D. pertusum</i>	3.8	0.4	-19.9	0.3
	<i>M. oculata</i>	3.3	0.9	-19.5	1.9
	<i>D. cornigera</i>	4.8	0.6	-21	0.5
$T_f$	<i>D. pertusum</i>	6.3	0.5	-20.7	0.8
	<i>M. oculata</i>	4.1	1.8	-20	1.7
	<i>D. cornigera</i>	6	0.6	-20.4	1.7

SD, standard deviation.

*cornigera* had the smallest total area (TA) (3.12 ‰<sup>2</sup>), followed by *D. pertusum* (4.12 ‰<sup>2</sup>), while *M. oculata* showed a TA of 16.2 ‰<sup>2</sup>. The corresponding values of the different SEA<sub>C</sub> are 2.75, 2.38 and 5.83 ‰<sup>2</sup>, for *D. pertusum*, *D. cornigera* and *M. oculata* respectively. While the SEA<sub>C</sub> of *M. oculata* and *D. cornigera* are expanded along the x-axis (pointing out to a wider  $\delta^{13}\text{C}$  range), the SEA<sub>C</sub> of *D. pertusum* is stretched along the y-axis (corresponding to a greater  $\delta^{15}\text{N}$  range) (Figure 4 and Table 3).

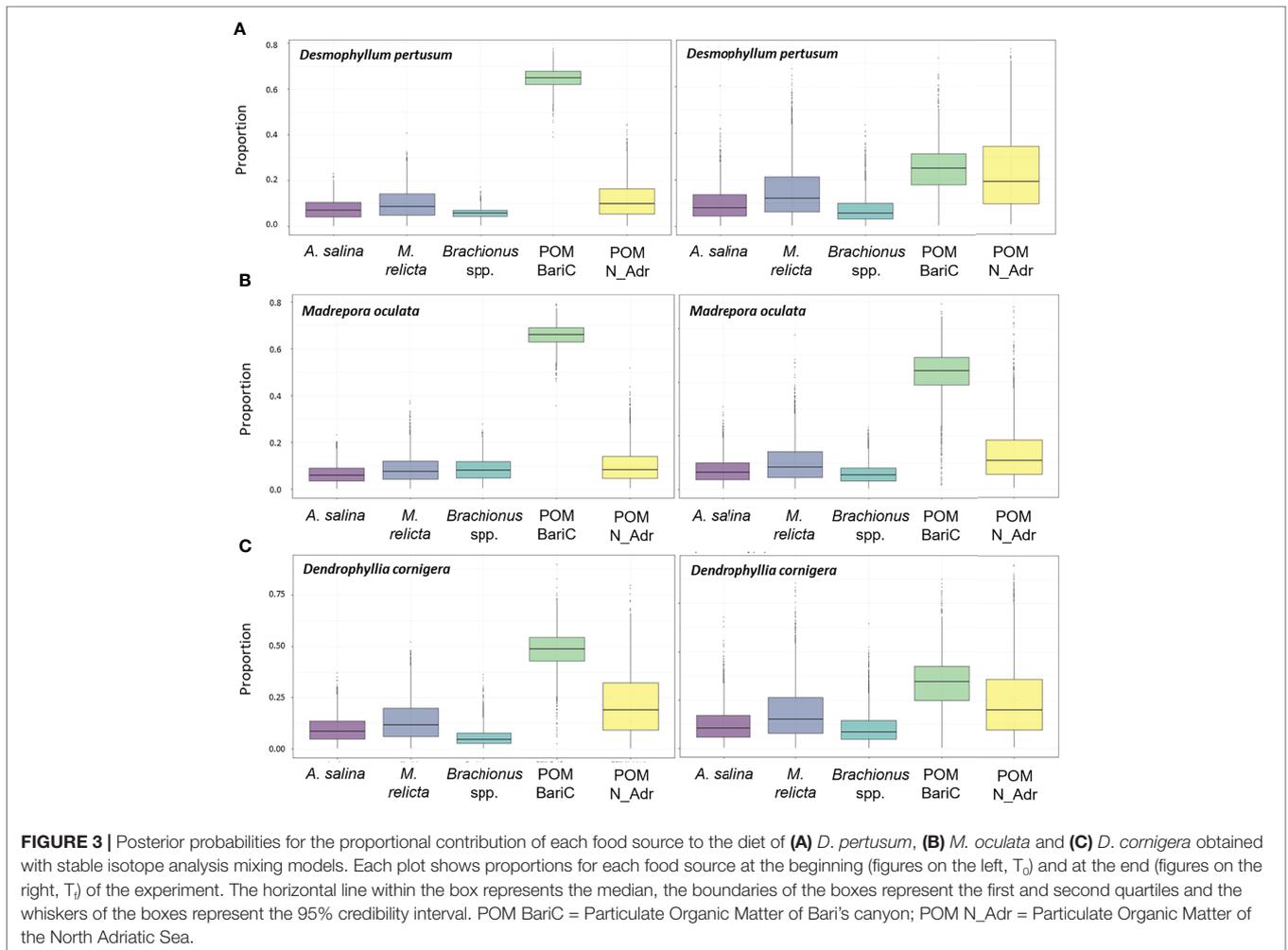
*M. oculata* has the greatest  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges and mean CD, which is a proxy of trophic diversity (Table 4). Overall, there is a partial overlap of the SEA<sub>C</sub> of the three species. The SEA<sub>C</sub> of *D.*

*pertusum* and *M. oculata* overlapped for 16.1%, while those of *D. pertusum* and that of *D. cornigera* for 15.4%. There is no overlap of the SEA<sub>C</sub> of *M. oculata* and *D. cornigera*.

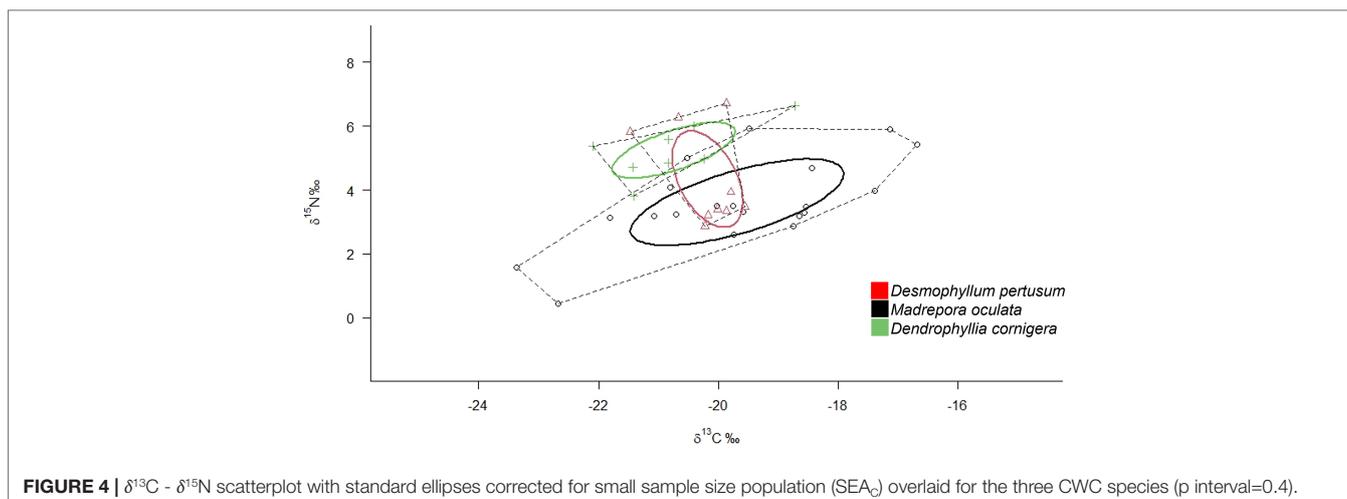
### 3.3 Prey-Capture Rates

Each polyp of *D. pertusum* captured an average of  $3.6 \pm 1.8$  (SE) nauplii of *A. salina* per hour,  $3.7 \pm 2$  (SE) individuals of *Brachionus* spp. and about  $3.2 \pm 0.7 \times 10^3$  (SE) cells of *T. subcordiformis*. Each polyp of *M. oculata* captured an average  $1 \pm 0.3$  (SE) nauplii of *A. salina* per hour,  $2.1 \pm 0.7$  (SE) rotifers and about  $9.8 \pm 2.6 \times 10^3$  (SE) cells of the algae. Each polyp of *D. cornigera* preyed, on average,  $2 \times 10^3 \pm 53$  (SE) nauplii per hour,  $1.6 \times 10^3 \pm 5.6 \times 10^2$  (SE) individuals of *Brachionus* spp. and about  $4.8 \pm 1.9 \times 10^4$  (SE) cells of algae (Table 4). Specimens of *M. relictata* were almost completely removed each time by all the three species of corals.

In terms of biomass, most of the organic carbon ( $\mu\text{g C polyp}^{-1} \text{ h}^{-1}$ ) was obtained by all the species from the largest preys (*M. relictata*,  $p < 0.01$  in the Tukey's post-hoc contrast tests; Table 4). Both *D. pertusum* and *D. cornigera* preyed a similar number of nauplii of *A. salina* and specimens of *Brachionus* spp., but the mass of carbon supplied by the crustaceans was higher ( $p > 0.05$ , not significant in the Tukey's post-hoc contrast tests) than that



**FIGURE 3** | Posterior probabilities for the proportional contribution of each food source to the diet of (A) *D. pertusum*, (B) *M. oculata* and (C) *D. cornigera* obtained with stable isotope analysis mixing models. Each plot shows proportions for each food source at the beginning (figures on the left,  $T_0$ ) and at the end (figures on the right,  $T_f$ ) of the experiment. The horizontal line within the box represents the median, the boundaries of the boxes represent the first and second quartiles and the whiskers of the boxes represent the 95% credibility interval. POM BariC = Particulate Organic Matter of Bari's canyon; POM N\_Adr = Particulate Organic Matter of the North Adriatic Sea.



**FIGURE 4** |  $\delta^{13}\text{C}$  -  $\delta^{15}\text{N}$  scatterplot with standard ellipses corrected for small sample size population ( $\text{SEAc}$ ) overlaid for the three CWC species ( $p$  interval=0.4).

of the rotifers. All coral species fed also upon *T. subcordiformis*, which provided a food supply higher ( $p > 0.05$ , not significant in the Tukey's *post-hoc* contrast tests) than that of the rotifers for the species *D. pertusum* and *M. oculata*.

## 4 DISCUSSION

This study investigated the food preferences of the CWCs, maintained in aquaria at conditions like those encountered during their life in the deep Mediterranean Sea. *D. cornigera* was the most reactive species, especially after the food supply that stimulates its polyps' reaction (Orejas et al., 2019). *D. pertusum* was the most sensitive species to the exposure, even to brief and weak-light expositions, such as those occurring during sampling operations. Being *D. pertusum* the species most closed to its ecological upper-temperature limit, probably it reacted stronger than the other species to this environmental stressor. Further studies are needed to further explore the role of light. Moreover, this species reacted slowly at the presence of food, confirming previous observations (Mortensen, 2001). Behaviour differences among species could possibly also reflect their reaction to variations in pressure from the site of collection to aquaria conditions, in the order of ca. 20 bars for *D. pertusum* and ca. 40 for *M. oculata* (Orejas et al., 2019). The eurybathic *D. cornigera* was instead collected at ca. 14 bars, thus facing lower pressure variations, in principle less stressing for the animal. *M. oculata* shows, in general, much higher tolerance

to environmental fluctuations (Wienberg et al., 2009), while *D. pertusum* is a species more commonly found in cold waters with temperatures between 4–12°C (Freiwald et al., 2004). In the central Mediterranean Sea, temperatures measured in live coral habitats during oceanographic campaigns range between 13.4 and 13.9°C (Freiwald et al., 2009). These temperatures are close to the ecological limit of *D. pertusum* (Brooke et al., 2013; Matos et al., 2021) while the optimal temperatures for this species were estimated to be around 6.2–6.7°C (Davies et al., 2008). These behavioural observations support the hypothesis that the temperature used during the experiments (13°C) was likely more suitable for *M. oculata* and *D. cornigera* (Naumann et al., 2014; Gori et al., 2015) than for *D. pertusum*.

During the whole experiment, the three CWC species captured all types of preys. Available literature data on feeding rates (Table S2) show that prey-capture rates differ among the three CWC species, depending also on the type of prey and on the different life stage of the specimens offered as food (e.g., naupliar stages vs. adults) as well as the temperature and the flow velocity under which the experiments are run.

In our study, prey-capture rates of the three species of CWCs showed a preference for the mysid *M. relicta*, and subordinately for the branchiopod *A. salina*. Several studies reported that the diet of CWCs in the field is based on zooplankton, such as copepods (Henrich and Freiwald, 1997; Kiriakoulakis et al., 2005; Naumann et al., 2015). *A. salina* has the same size of these target copepods (Orejas et al., 2019 and references therein). Among the three different species, *M. oculata* is the one with smallest polyps (5–10 mm in diameter) (Orejas et al., 2019), so the greater capture rates for rotifers (around 350  $\mu\text{m}$  in length) appears as the result of the selection of a prey with a suitable size compared to the size of the corals' polyps.

Comparing measurements of prey-capture rates from different experiments is difficult because capture rates may overestimate the real ingestion rate if the prey is not efficiently transferred to the gut (Purser et al., 2010). Trapped food may be partly lost due to the sloppy feeding (Møller, 2004) or could not be assimilated, so prey-capture rates cannot directly be translated into ingestion

**TABLE 3** | Total area (TA,  $\% \text{‰}^2$ ), Standard ellipse area ( $\text{SEAc}$ ,  $\% \text{‰}^2$ ) and Layman metrics calculated for each species.

	<i>D. pertusum</i>	<i>M. oculata</i>	<i>D. cornigera</i>
TA	4.12	16.20	3.12
SEAc	2.75	5.83	2.38
$\delta^{15}\text{N}$ range	3.85	5.46	2.80
$\delta^{13}\text{C}$ range	1.92	6.68	3.38
CD	1.39	1.79	1.05

**TABLE 4** | Different prey-capture rates of the three species of corals and total quantity of carbon captured per polyp.

Species	Food source	Prey-capture rate (ind polyp <sup>-1</sup> h <sup>-1</sup> ) ± SE	Total C (μg C polyp <sup>-1</sup> h <sup>-1</sup> ) ± SD
<i>D. pertusum</i>	<i>M. relicta</i>	0.004 ± 2 × 10 <sup>-4</sup>	14.2 ± 7.12
<i>D. pertusum</i>	<i>A. salina</i>	3.6 ± 1.8	0.8 ± 0.44
<i>D. pertusum</i>	<i>Brachionus</i> spp.	3.7 ± 2	0.3 ± 0.17
<i>D. pertusum</i>	<i>T. subcordiformis</i>	3.2 ± 0.7 × 10 <sup>3</sup>	0.7 ± 0.16
<i>M. oculata</i>	<i>M. relicta</i>	0.001 ± 2 × 10 <sup>-4</sup>	3.6 ± 0.71
<i>M. oculata</i>	<i>A. salina</i>	1 ± 0.3	0.2 ± 0.07
<i>M. oculata</i>	<i>Brachionus</i> spp.	2.1 ± 0.7	0.2 ± 0.06
<i>M. oculata</i>	<i>T. subcordiformis</i>	9.8 ± 2.6 × 10 <sup>3</sup>	0.2 ± 0.05
<i>D. cornigera</i>	<i>M. relicta</i>	0.2 ± 0.01	783.2 ± 35.6
<i>D. cornigera</i>	<i>A. salina</i>	2 × 10 <sup>3</sup> ± 53	47.2 ± 12.60
<i>D. cornigera</i>	<i>Brachionus</i> spp.	1.6 × 10 <sup>3</sup> ± 5.6 × 10 <sup>2</sup>	13.9 ± 4.85
<i>D. cornigera</i>	<i>T. subcordiformis</i>	4.8 ± 1.9 × 10 <sup>4</sup>	10 ± 3.89

ind, individuals; SE, standard error; SD, standard deviation.

rates or even in assimilation rates (Orejas et al., 2019). Because of this, we integrated capture-rates results with SIA outcomes to determine the assimilated food.

The values of  $\delta^{13}\text{C}$  measured at  $T_0$  in this study for the three CWCs species (from -21 to -19.5 ‰) fit well with that of North Atlantic CWCs (from -22.2 to -19.3 ‰) (Duineveld et al., 2004; Sherwood et al., 2008). These values are slightly more negative than that for CWCs from the Strait of Sicily, South of Malta (from -18.9 to -18.2 ‰, CNR cruise CORAL of the RV 'Urania', 450–600 m) (pers. comm. M. Taviani), but this can be justified by the different characteristics of the Adriatic basin and of the Sicily Strait (higher salinity and temperature of this latter, Simoncelli et al., 2014), which typically influence the isotopic composition of the POM (Fanelli et al., 2013; Conese et al., 2019). Our results are consistent also with data from the CWCs coral province of Santa Maria di Leuca for *D. pertusum* and *M. oculata* ( $\delta^{13}\text{C}$  from -19 to -21 ‰) (Carlier et al., 2009). In our experiment, a decrease in  $\delta^{13}\text{C}$  in *D. pertusum* and *M. oculata* was observed at  $T_p$ , although  $\delta^{13}\text{C}$  values remain like those reported for the Ionian Sea (Carlier et al., 2009). These results likely support the hypothesis of a high similarity, in terms of food sources, between the South Adriatic (Bari Canyon) and S. Maria di Leuca CWC provinces. On the contrary, an increase in  $\delta^{13}\text{C}$  for *D. cornigera* was observed probably due to the preferential ingestion of *M. relicta*. The polyps of this coral measure 20–40 mm in diameter (Orejas et al., 2019) and mysids are likely more suitable to the dimensions of this species (Gori et al., 2015; Orejas et al., 2019).

The values of  $\delta^{15}\text{N}$  at  $T_0$  in all the species were more negative (about halved) than those obtained for *D. pertusum* and *M. oculata* analysed in the Santa Maria di Leuca CWC province (values of  $\delta^{15}\text{N}$  from 6.9 to 10.1 ‰) (Carlier et al., 2009) or in the Atlantic (Duineveld et al., 2004; Kiriakoulakis et al., 2005). The  $^{15}\text{N}$ -depletion could be caused by both thermal shocks that occurred during the recovery from the seabed, and/or by light exposure and decompression (Orejas et al., 2019). In fact, corals started eating only after a period of acclimation. The results from the simmr mixing model show that at  $T_0$ , all the three investigated species had an isotopic composition close to that of the POM of the region (i.e., the Bari Canyon; Carlier et al., 2009). POM is easier to consume and less energy-expensive to

capture compared to whole animal preys (living or frozen), so our results confirm that CWCs are able to use also fine organic particles as food source (Mortensen, 2001; Mueller et al., 2014; Orejas et al., 2016). These results suggest that corals filtered POM from surrounding seawater. It is probable that CWCs can sustain their basal metabolism feeding only on POM when other food sources are not available. As an example, the values of  $\delta^{15}\text{N}$  of *D. pertusum* and *M. oculata* in the Rockall Bank are very close to that of obligate filter-feeding taxa like tunicates and bivalves that are known to feed only on organic particles (Duineveld et al., 2007). In our experiment, after 30 days, the isotopic values of corals reared in aquaria were closer to those of POM of the northern Adriatic Sea that is probably incorporated in their soft bodies faster than the other food sources. Among them, according to simmr results, the mysids *M. relicta* contributed to the corals' diet for ~17%. This prey seemed to be the preferred one, also in terms of feeding rates. This crustacean is a member of the family Mysidae, the same family of *Boreomysis arctica* (Krøyer, 1861) and *B. megalops* (G.O. Sars, 1872) that are among the most abundant supra-benthic species on the upper and middle slope of the Ionian (Madurell and Cartes, 2003) and the Catalan Sea (Cartes et al., 2011), and are likely among the main natural preys of CWCs living in these areas. Considering together results of prey-capture rates and results of SIA allows to suggest that the maintenance in aquaria of CWCs could be optimised by a diet based on the supplying of frozen *Mysis* sp. instead of the most common used and live-prey *A. salina*. Supplying the corals with *Mysis* sp. can also solve the problem of the depletion of some components, like fatty acids, in the tissue of corals fed only with *A. salina* (Larsson et al., 2013). Discrepancies between prey-capture rates and the degree of assimilation of the food sources in the soft bodies of the corals should be correlated with the utilization of the ingested food for respiration, for maintenance and growth, tissue growth and storage, reproduction and the release of mucus as dissolved organic matter (Orejas et al., 2019) that can also be re-ingested and assimilated as a strategy to withstand several months without food supply (Mueller et al., 2014).

*M. oculata* seems to be a more generalist species, with the greatest trophic diversity, as evidenced by the wide  $\delta^{13}\text{C}$  range and the greatest CD values, and the highest feeding plasticity compared

to the other two CWC species. A generalist behaviour in deep-sea ecosystems represents an advantage, as the species can rely on available food source (POM, zooplankton, phytodetritus) in an environment where food availability may be heterogeneous in time and space (Gori et al., 2018). Opportunistic feeding behaviour was previously reported for *D. pertusum* (Mortensen, 2001; van Oevelen et al., 2009; Mueller et al., 2014; Orejas et al., 2016), *M. oculata* and *D. cornigera* (Gori et al., 2018). In the Mediterranean basin, *M. oculata* seems to be the most abundant CWC species: it is up to 50 times more abundant than *D. pertusum* in Cap de Creus and Lacaze-Duthiers canyons in the Gulf of Lion (Gori et al., 2013), exclusively present in the eastern Ligurian sea (Fanelli et al., 2017), and dominates the CWC communities in the Santa Maria di Leuca coral province (Vertino et al., 2010), in Bari Canyon (Freiwald et al., 2009) and in the Alboran Sea (Corbera et al., 2019). The higher abundance of this species in the basin may be related also to its greater range of food items and its wider ability to exploit different food sources.

## 5 CONCLUSIONS

There is growing evidence that conservation measures alone, such as the creation of offshore MPAs or Fishery Restricted Areas (FRAs), albeit necessary to avoid the negative effects of the bottom trawling (Huvenne et al., 2016), are not sufficient to protect these vulnerable habitats from the numerous synergistic impacts that threaten them (Ragnarsson et al., 2016). Moreover, it is known that CWC colonies are slow growing species, which require decades to reach a diameter of 1.5–2 m and possibly thousands of years to build a reef (10–30 m thick; Fosså et al., 2002). Due to their low growth rates, the expected natural recovery rates can be very slow.

Active restoration actions for CWC reefs will require rearing and/or maintenance in aquaria of nubbins taken from healthy donor colonies and transplantation of these fragments into degraded mounds (Van Dover et al., 2014). Promising results of pilot transplantation experiments have been reported in literature for *D. pertusum* (Da Ros et al., 2019 and references therein). The outcomes of our experiments confirm that it is possible to maintain CWCs in aquaria and allow us to identify the best feeding conditions to keep them in aquaria. Our study provides novel information on the trophic items preferred by *D. pertusum*, *M. oculata* and *D. cornigera* in the Mediterranean Sea. Maintaining corals in aquaria and improving their wellness in captivity may positively impinge on their growth or reproduction success, which may turn into the generation of nubbins successfully

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transplantable in degraded reefs. Additionally, transplanting healthy corals will increase the chances of obtaining a positive outcome of the effort made, thus contributing to the achievement of the goal of a successful restoration of degraded ecosystem as several frameworks and directives foresee for the next future.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**. Further inquiries can be directed to the corresponding authors.

## AUTHOR CONTRIBUTIONS

RD, MT, AD'A conceived the study. RD, MT, EF and AD'A designed the sampling strategy. LA and MT performed the sampling. ZDR and EF analysed the samples. ZDR and EF performed the statistical analyses. ZDR wrote the original draft of the paper, with contributions from EF, RD, MT, ADA and LA revised the original draft. All authors have read and agreed to the published version of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.867656/full#supplementary-material>

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