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Cold-water coral Dendrophyllia ramea as a habitat-forming species in shallow coastal waters: its role in a vulnerable ecosystem and anthropogenic impacts

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Abstract

The importance of habitat-forming species, particularly cold-water corals like Dendrophyllia ramea, cannot be overstated as they provide crucial physical structures that offer shelter, food, and breeding habitat for a range of other species. We studied the spatial distribution and abundance of D. ramea, its associated species and the impact of human activities in a population of the Herradura, Granada in the western Mediterranean. Video transects were conducted at different depths, and epibiont samples were collected to describe the coral assemblage and the diversity of associated organisms. Dendrophyllia ramea presented high abundances at an unusually shallow depth in the Mediterranean, ranging from 30 to 48 m, despite typically being found between 50 and 500 m, with recordings indicating occurrences as deep as 1000 m, and hosting a high number of epibionts and macro-benthic organisms associated with coral reefs. Bryozoans showed a close relationship with D. ramea as they are important components of both the reef and the epibiont community. This study identified 63 new species and 15 new genera associated with cold-water corals. This study showed the importance of D. ramea as a nursery site, even for other habitat-forming species. The major threat to this community is human activity (fishing, littering and free anchoring), with the most abundant types of waste being rubber, glass/ceramics, and plastic polymers, and many fishing lines and nets damaging the corals. Overall, this study emphasises the urgent need to protect cold-water corals and their associated species and reduce the impact of human activities on marine ecosystems.

Introduction

Habitat-forming species (HFS) play a crucial role in shaping communities by creating stable conditions for other species and influencing the processes within those ecosystems (Dayton, [1972;](#page-9-0) Stachowicz, [2001](#page-10-0); Crain and Bertness, [2006\)](#page-9-0). Therefore, they are of great environmental importance due to their contribution in maintaining biodiversity and ecosystem function (Bulleri et al., [2018](#page-9-0)). The loss of these species can have a dramatic effect on natural habitats with consequences on associated biota, ecosystem function and stability (Ellison et al., [2005](#page-9-0)).

Cold-water corals (CWC) are considered HFS because they exhibit complex branching morphology and sufficient size to provide substrate and/or shelter for other species (Freiwald and Roberts, [2005\)](#page-9-0). Indeed, coral systems have a wide ecological relevance, given the large number of interactions that occur in them (Díaz et al., [1996](#page-9-0)). CWC play an important structural and functional role (Wildish and Kristmanson, [1997](#page-10-0)), as they are engineers of deep-water ecosystems (Jones et al., [1994](#page-10-0)) and are found in all oceans (Freiwald et al., [2004\)](#page-9-0). In addition, organisms provide structurally complex that allows for greater diversity than in areas where they are not found (Buhl-Mortensen et al., [2010](#page-9-0)).

The distribution and abundance of CWC in the marine benthos is the result of evolutionary processes, environmental conditions, the extent of the ecological niche of each species and the dynamics of each coral population, which, in turn, are determined by the ecological rela-tionships between the species that coexist in that environment (Brown, [1995](#page-9-0); Lo Iacono et al., [2019\)](#page-10-0). These parameters are defined by the specific bathymetric range in which each group of organisms is distributed, which in turn depends on the geomorphology of the location (Chimienti et al., [2019\)](#page-9-0).

Several CWC species have inhabited the Mediterranean Sea since the Miocene epoch, experienced significant changes over time (Altuna and Poliseno, [2019\)](#page-8-0). Seabed complexity, determined by the physical and chemical properties of the water column, is an important factor contributing to the distribution and development of CWC communities in this Sea (Hayes et al., [2019](#page-10-0)). However, few studies provide a spatial context for CWC habitats in the Mediterranean and more data from less explored areas are needed to better define their overall regional distribution and relate them to environmental factors (Lo Iacono et al., [2019\)](#page-10-0). In some parts of the Mediterranean and adjacent areas (e.g. Strait of Gibraltar, Gulf of Cadiz) the CWC-associated fauna is not well known (Lastras et al., [2019\)](#page-10-0). As a consequence, the lack of knowledge about the ecology of these species undermines conservation efforts (Enrichetti et al., [2023\)](#page-9-0).

Dendrophyllia ramea (Linnaeus 1758), is an anthozoan of the order Scleractinia, belonging to the family Dendrophylliidae. This species is distributed in most of the Mediterranean Sea and in the Atlantic Ocean (Zibrowius, [1980](#page-11-0)). The presence of D. ramea has been recorded mainly in the Western Mediterranean basin, on the Italian coasts from the Sea of Sicily (Salvati et al., [2021;](#page-10-0) Angiolillo et al., [2022](#page-8-0)) to the Gulf of Naples (Zibrowius, [1980\)](#page-11-0), on the Catalan coasts of the Balearic Sea (Sánchez et al., [2004](#page-10-0)) and the Gulf of León (Zibrowius, [1980](#page-11-0)); as well as in the Alborán Sea (Zibrowius, [1980;](#page-11-0) Ocaña et al., [2000;](#page-10-0) Cebrián and Ballesteros, [2004\)](#page-9-0). Recently, this species was found attached to soft sediments (Salomidi et al., [2010](#page-10-0); Orejas et al., [2017](#page-10-0)), though usually D. ramea in the Mediterranean was considered to be associated with rocky substrates. This suggests that its distribution could be wider than considered so far. In the Atlantic Ocean, it is present in Portugal (Zibrowius, [1980](#page-11-0)), on the Atlantic coast of Morocco (Patriti, [1970;](#page-10-0) Zibrowius, [1981\)](#page-11-0), the Canary Islands (Brito and Ocaña, [2004\)](#page-9-0), Western Sahara, Senegal (Chevalier, [1966\)](#page-9-0), the Azores, Cape Verde, Ghana, the Gulf of Guinea and Nigeria (Zibrowius, [1980\)](#page-11-0).

Additionally, D. ramea has been classified as 'Vulnerable' in the Red List of Threatened Species of the Mediterranean by the International Union for Conservation of Nature (IUCN) and has also been included in the list of endangered or threatened species in Annex II of the Mediterranean Action Plan (MAP) of the Barcelona Convention. Because of its scarcity and deep bathymetric distribution, this coral is listed as 'Vulnerable' to extinction by the Red Data Book of Invertebrates in Andalusia, which is included in Appendix II of the CITES Convention. However, it is not included in the National Catalogue of Endangered Species because there is no scientific basis on the status of its populations to justify the necessity of protection. This fact highlights the urgent importance of carrying out this type of study to characterise its populations.

The Special Conservation Zone of Seabeds and Cliffs of Punta de la Mona is an area located in La Herradura (Granada, Spain), where the presence of cliffs and seabed form a favourable habitat for the growth of D. ramea (Cebrián and Ballesteros, [2004\)](#page-9-0) and it constitutes one of the westernmost points of distribution for this species in the Mediterranean Sea (Salvati et al., [2021\)](#page-10-0). The cover-age of these corals hosts a high biodiversity (Longo et al., [2005](#page-10-0); Mastrototaro et al., [2010](#page-10-0)), providing shelter for other species, as well as suitable substrate for the recruitment and adults settlement of associated species (Baillon et al., [2012](#page-8-0); Rueda et al., [2019\)](#page-10-0). Therefore, the environmental and biological complexity provided by D. ramea is fundamental for the development of a hotspot. From this, it is inferred that the study of the structure and distribution of this assemblage is of utmost importance to develop assertive management and conservation plans. However, in the Alboran Sea, the species associated with CWC are still not well characterised (Rueda et al., [2019](#page-10-0)).

Due to this, it is important to understand what role D. ramea plays in the ecosystem, its bathymetric distribution and density patterns. Additionally, the size ranges could provide information on the abundance of juveniles or adults, which, if studied at different depths, would help to infer the colonisation processes that this species undergoes (Guzmán and Guevara, [1998\)](#page-10-0). Although this cnidarian is a dominant species in the study area below depths of 20 m (Cebrián and Ballesteros, [2004\)](#page-9-0), the

distribution patterns of this assemblage and the size structure are not yet well described in this area.

For several years now, anthropogenic pressure on a global scale has been causing the deterioration of CWC habitats and, as a consequence, the decline of entire biological communities (Haapkylä et al., [2007](#page-10-0); Hoegh-Guldberg, [2011;](#page-10-0) Eakin et al., [2019\)](#page-9-0). The environments inhabited by D. ramea harbour high biodiversity and biomass, so fishing pressure is significantly higher compared to adjacent areas (Buhl-Mortensen et al., [2010](#page-9-0)). Trawling particularly affects these populations, both in their size structure, age composition, abundance and structural complexity (Clark and Koslow, [2007\)](#page-9-0).

Due to the current lack of information on this species (Salvati et al., [2021\)](#page-10-0) and its importance for marine biodiversity locally and regionally, the aims of this study were: (1) to survey the bathymetric distribution, abundance and size ranges of the coral species D. ramea in the coast of Granada; (2) to study the non-epibiotic communities (hereafter, macro-benthonic communities) associated with this HFS; (3) to assess the epibionts on D. ramea; (4) to evaluate the marine litter and possible threats to the D. ramea assemblage; and (5) to provide information to help in the development of an appropriate management and conservation plan.

Materials and Methods

Study area

The study area was the Special Conservation Zone of Seabeds and Cliffs of Punta de la Mona (PM hereafter), on the Northern coast of the Alboran Sea ([Figure 1](#page-2-0)). In terms of its ecosystem importance, this place was catalogued among the 'Zonas Especiales de Conservación con Hábitats Marinos del Litoral Andaluz' (Special Conservation Zones with Marine Habitats on the Andalusian Coast), a Marine Protected Figure recognised by the Spanish government, and has been included in the 'Red Natura', classified as a site of community interest.

Dendrophyllia ramea assemblage description

The seabed of Punta de la Mona hosts a wide variety of habitats. In the deeper regions, a reef dominates the landscape, extending through three southeast-oriented underwater canyons with vertical limestone walls. These walls descend to a soft sandy substrate at depths reaching −48 m. The rocky substrate is continuous throughout the area, but marine currents and upwellings resuspend the soft substrate in the deep zone, creating small, mobile sandbanks on the canyon floors.

In the study area, a survey was carried out by SCUBA diving rebreather and videos. Video transects, 50 m long and 1.5 m wide, were performed at a constant speed, 1 m above the seabed parallel to the coastline, every 6 m in depth from 30 to 48 m. Three random video transects were recorded per depth (see [Figure 1](#page-2-0)). The survey took place in April 2021. To estimate the abundance, size and distribution of D. ramea in the study area, the number of colonies and branches were counted, as well as the coverage of each colony by analysing the images obtained from the videos with ImageJ software (version 1.4.3.67). For the scale reference, a special system was designed with a scooter support, consisting of two lasers pointing at a known distance of 1.5 m.

To study the D. ramea assemblage, the number of colonies and branches per transect were analysed using a generalised-linear model (GLM). The cover of colonies per transect was analysed using a linear model analysis (LM). These variables were considered a response variable and 'Depth' was a fixed factor with four levels: 30, 36, 42 and 48 m.

Figure 1. Study area: (A) Mediterranean Sea; (B) northern coast of the Alboran Sea; (C) bathymetry of the seabed at Punta de la Mona showing the locations of the video transects and epibiont sampling sites.

Macro-benthic communities

Visual identification of the macro-species associated with the D. ramea reef was determined from the sampling videos (see Figure 1). To study the composition, structure, and diversity of these benthic communities at each depth, the abundance of the individuals was estimated by frequency of occurrence (Bianchi et al., [2004\)](#page-8-0).

The number of species of the macro-benthic community per transect was analysed using GLM. To study the multivariate structure of the community of macro-benthic organisms associated to D. ramea reef, a Permuted Multivariate Analysis of Variance (PERMANOVA) (Anderson, [2001;](#page-8-0) McArdle and Anderson, [2001\)](#page-10-0) was used, where the data were organised into species/abundance matrices, considering the experimental design previously explained. Abundance values were square-root transformed to prevent highly abundant species from overly influencing the analyses and causing the contribution of less abundant species to be insignificant (Clarke and Warwick, [2001](#page-9-0)). To determine the percentage contribution of each taxon or species to the similarity measures within the 'Depth' factor levels, the SIMPER (Similarity Percentage; Clarke, [1993\)](#page-9-0) similarity partitioning analysis was used. The homogeneity of variances was also tested with the PERMDISP test (Anderson, [2006](#page-8-0)).

Epibiont community

Epibiont samples were taken using a scraping technique, where a scalpel blade was arranged perpendicular to the surface of the coral, so as not to damage its living tissue and, with a sample bottle, the mass of epibiont dragged in each scraping was collected. It's important to note that mobile species might have had the chance to escape during this process. Due to the time needed to sample epibionts without damaging the *D. ramea* colonies and the difficulty of diving deeper than 40 m, the number of transects were reduced. The depths for sampling were selected to be intermediate to those of the video transects (see Figure 1). Eight samples were collected along each three 100 m long transects at three different depths: 34, 40, and 45 m (making a total of 24 samples). The samples were fixed in 96% ethanol and subsequently analysed in the laboratory under binocular magnification and optical

microscopy. Organisms were identified to the highest possible taxonomic resolution, in most cases to the species level.

The number of species of epibionts per depth was analysed using GLM and the multivariate structure of the epibiont community was tested using PERMANOVA. In this case, the experimental design considered the presence/absence of organisms at 'Depth' with three levels (34, 40, and 45 m). The homogeneity of variances was also tested with the PERMDISP analysis.

Threats to the integrity of the CWC habitat: marine litter on the seafloor

In addition, the recognition and description of the types of litter according to each category, according to Fleet et al., [2021](#page-9-0), and the debris coverage present in the area, were used to estimate the anthropogenic impact suffered by these communities of organisms. The litter was classified on Rubber, Glass/Ceramic, Cloth/ Textile, Artificial Plastic Polymers (predominantly originating from fishing activities) and Metals, considering five main categories of materials (Fleet et al., [2021](#page-9-0)). The litter coverage per transect was analysed using LM and considering two fixed factors: 'Depth' with four levels (30, 36, 42, and 48 m) and 'Type of litter' with five levels (the categories previously named). The normality and homogeneity of the residuals were checked with a Shapiro–Wilk and Bartlett's tests, respectively. The coverage of each of these categories was plotted in a bar chart separated by depth.

Univariate analyses (LM and GLM) were carried out with the R software version v4.1.1 (CoreTeam R, [2021](#page-9-0)). To make the graphs, the 'ggplot2' package (Wickham, [2016\)](#page-10-0) was used. All multivariate analyses were carried out with PRIMER-E v6.1.11 and PERMANOVA+ v1.0.1 software (Clarke and Gorley, [2006](#page-9-0)).

Results

D. ramea assemblage at PM

In the study area, a total of 311 colonies of D. ramea were identified and distributed as follows: 25 colonies at a depth of 30 m, 178 at a depth of 36 m, 93 at 42 m, and 15 colonies at a depth of 48 m. The mean number of colonies per transect showed the existence of two groups of depths: one formed by the intermediate

(36 and 42 m) depths and the other formed by the extreme depths (30 and 48 m), which showed significant differences between them (Table 1). Colonies exhibit variable coverage, ranging from 2300 cm² to some individuals of only 3 cm², consisting of a single polyp. There was a greater number of individuals with smaller coverage than with larger coverage, a pattern that is followed throughout the depth gradient studied [\(Figure 2A](#page-4-0)). In addition, coral abundance at 36 and 42 m was higher than the remaining depths, which is consistent with the zone with the greater number of colonies. However, these differences were not statistically significant. Furthermore, it can be observed that the colonies contain a lower number of branches at 30 and 48 m ([Figure 2B](#page-4-0)), although the differences between depths were also not significant.

Macro-benthic community

A total of 47 species belonging to 9 taxonomic groups were identified in the study area, which characterised the organisms associated to D. ramea reef (Table S1). According to the nMDS graph, there is a transition in this benthic community with a zonation pattern as a function of depth gradient. The composition and abundance of species associated with the coral assemblage at 48 m deep is clearly different from the other depths [\(Figure 3\)](#page-5-0) and follows a gradient determined by the bottom depth. The multivariate PERMANOVA analysis showed that there are significant differences in the composition and abundance of the species at the analysed depths [Pseudo- $F_3 = 6.30$; $P(\text{perm}) = 0.001$].

The a posteriori PERMANOVA analysis showed the existence of three groups: one composed of the depths of 30 and 36 m together, another with a depth of 42 m and the last group with a depth of 48 m [\(Table 2\)](#page-5-0). No dispersion problems were found in the study [PERMDISP: $F_3 = 2.97$; $P(\text{perm}) = 0.1$].

From the SIMPER analysis, it was found that 17 species are the ones that contribute the most to the differences found between depth groups, with 13 of them corresponding to the group of 30 and 36 m, 14 to 42 m, and 10 to 48 m (Table S2). Among these species, those that were common at all depth groups with similar abundances were: the gorgonia Eunicella verrucosa (Pallas, 1766), the porifera Aplysina aerophoba (Nardo, 1833), Crambe crambe (Schmidt, 1862), and Timea sp. The most abundant species that characterised the depth groups of 30 and 36 m were: the algae Mesophyllum alternans (Foslie), Cabioch and M. L., Mendoza, 1998 or the bryozoans Myriapora truncata (Pallas, 1766) and Pentapora fascialis (Pallas, 1766); at 42 m: Axinella damicornis (Esper, 1794) or Parazoanthus axinellae (Schmidt, 1862); and at the 48 m level: the sponges Cliona viridis (Schmidt, 1862) or Haliclona (Reniera) mediterranea Griessinger, 1971.

When analysing the variation in the number of species that make up the community macro-benthic organisms the number of species did not differ significantly between the different depth groups. In any case, it can be observed that the number

Table 1. Generalised Linear Model for the mean number of Dendrophyllia ramea colonies per depth (m).

| | Estimated | SE | z value | P value |
|-----------|-----------|-----------|---------|----------------------|
| Intercept | 21.20 | 0.20 | 10.60 | $\leq 0.001^a$ |
| 36 | 19.63 | 0.21 | 9.19 | < 0.001 ^a |
| 42 | 13.14 | 0.22 | 5.83 | $\leq 0.001^a$ |
| 48 | -0.51 | 0.33 | -1.56 | 0.118 |

SE, standard errors.

For the categorical variable 'Depth', 30 m was used as reference level. ^aSignificant differences at $P < 0.05$.

of species is lower at 48 m with respect to the other depth groups. However, the depths of 30 and 36 m showed similar values of diversity, the 42 depth showed the higher number of species and the 48 m depth the lower values of diversity [\(Figure 4\)](#page-6-0).

Epibiont community

A total of 88 epibiont taxa associated with D. ramea, belonging to 12 different taxonomic groups, were identified (Table S1). The nMDS graphical representation shows that the composition of the epibiont community varies according to the depth gradient. It seems that the species composition corresponding to the extreme depths are different from each other, while at the intermediate zone the communities are in a transitional position, with no differences in the other two depths ([Figure 5](#page-6-0)). The PERMANOVA analysis showed that there are significant differences in the composition of the species of epibiont at the analysed depths [Pseudo- $F_2 = 1.72$; $P(\text{perm}) = 0.017$]. The *a posteriori* analysis confirmed that there are differences in the composition of this community in the shallowest zone (34 m) in relation to the deep zone (45 m), while the intermediate depth (40 m) showed no difference to the previous ones ([Table 3\)](#page-7-0). No dispersion problems were noted in the study [PERMDISP: $F_2 = 1.64$; $P(\text{perm})$ $= 0.276$].

In accordance with the SIMPER analysis (Table S3), 20 species of epibionts contributed to the differences between the depths of 34 and 45 m. Of these species, 11 were those that characterised the first depth, and 12 species characterised the second. The only organism common to all depths analysed (34, 40, and 45 m), with analogous similarities, was the bryozoan Cellepora pumicosa (Pallas, 1766). The species that characterised the depth of 34 m, with higher similarities, were juveniles and recruits of the bivalve Gregariella semigranata (Reeve, 1858), the bryozoan of genus Bugula Oken, 1815 or the echinoderm of genus Ophiura Lamarck, 1801. For the depth of 45 m, the hydrozoans Campanularia hincksii Alder, 1856 and Clytia linearis (Thorneley, 1900) or the sponge Hymedesmia sp. were characteristic. Finally, the species that presented analogous similarities and that contributed to the fact that the depth of 40 m is not different from that of 34 m were: the amphipods from the families Caprellidae, Ischyroceridae, Aoridae, Sthenothoidae, Dexaminidae, and Corophiidae, alongside the hydrozoan Laomedea sp.; and at the depth of 45 m: the bryozoan Pentapora fascialis and the poriferous Timea sp.

In congruence with the multivariate analysis, the number of species of epibionts showed similar results. It is lower in the shallowest zone (34 m) compared to the deepest area studied (45 m) and the intermediate depth (40 m) showed no significant difference with any of the previous ones ([Figure 6\)](#page-7-0).

Threats to the integrity of the CWC habitat: marine litter on the seafloor

The anthropogenic impact on the study area was evaluated by analysing the coverage of litter, which showed the highest average coverage at a depth of 42 m and a lowest coverage at 48 m. Artificial polymers (plastics from fishing waste, such as nets, ropes, fishing lines and to a lesser extent, and plastic bags) had the largest average litter coverage (cm²), but high amounts of glass (bottles) and ceramic debris, fabric and textile debris, metals (from free anchorages) and rubber were also identified [\(Figure 7](#page-7-0)). In our video observations, we noted that a significant portion of marine litter originated from longlines and other gears used in fishing activities. The results of the LM analyses showed significant interactions between the factors 'Depth' and 'Type of litter' $(F_{12} = 2.99; P = 0.004)$, indicating that the differences in cover of each type of litter were not homogeneous across levels of the

Figure 2. Dendrophyllia ramea assemblage in Punta de la Mona: (A) coverage values (cm²); (B) number of branches per depth (m).

factor 'Depth'. The transects spanned a total length of 100 m at each depth of 30, 36, 42, and 48 m, positioned at distances from the coastline as shown in the map [\(Figure 1](#page-2-0)). Given the significant interactions, the analyses were conducted by type of litter. Only artificial plastic polymer showed significant differences among depths. The lowest abundance of artificial plastic polymers was recorded at 48 m, the highest at 42 m, and its coverage at 36 m was also significantly different from that at 48 m, although this result was only marginally significant ([Table 4\)](#page-7-0). Furthermore, it was found that 73% of the total colonies were entangled in ropes or human debris, resulting in various types of harm or impairment.

Discussion

The present study quantitatively describes Dendrophyllia ramea assemblage in Western Mediterranean area, at the locality of PM, considering abundance, colony size range, and distribution

Figure 3. nMDS representing the differences in the community of macro-benthic organisms associated with Dendrophyllia ramea per depth (m). Stress = 0.05.

patterns, as well as the diversity of organisms associated with it and the anthropogenic impact. In this area, the 311 colonies surveyed (representing only a fraction of a much larger population, pers. obs.) exhibited a greater abundance at a depth unusually shallow in relation to that recorded so far (40–400 m) in the Mediterranean Sea (Bonfitto et al., [1994;](#page-9-0) Kružić et al., [2002](#page-10-0); Requena and Gili, [2014\)](#page-10-0).

The D. ramea assemblage in the four depths selected in this study seems to be conditioned by the mixing of water masses from the Atlantic Ocean with those from the Mediterranean Sea. The Alboran Sea is highly influenced, on one hand by the inflowing Atlantic waters (Candela, [1991](#page-9-0)), which presents an asymmetric circulation through the Strait and through the Alboran Sea (Echevarría et al., [2002;](#page-9-0) Skliris and Beckers, [2009\)](#page-10-0). The Atlantic water passes eastward along the northern part of the Alboran Sea (the Atlantic Jet) and forms 2 anticyclonic gyres (Western Alboran Gyre and Eastern Alboran Gyre) which reach the African Coast (Millot, [1992;](#page-10-0) Vargas-Yáñez et al., [2002\)](#page-10-0). On the other hand, the northern coast of the Alboran Sea, is also influenced by Mediterranean Water (Northern Current), coming from the Catalan Sea, and running down the Spanish Mediterranean Coast towards the Strait of Gibraltar (Bouzinac et al., [2003\)](#page-9-0). This water mass loses its influence close to the Strait (there, the Atlantic Jet blocks it; Sarhan et al., [2000\)](#page-10-0), and it seems to give a typical Mediterranean character to the northern coast. Thus, Alboran Sea presents intermediate condition between Atlantic and Mediterranean in regard to dissolved nutrients and plankton biomass (Gómez et al., [2000\)](#page-9-0), sea surface temperature, and sea level (Bouzinac et al., [2003](#page-9-0); Nykjaer, [2009\)](#page-10-0).

Table 2. A posteriori pair-wise permutation multivariate analysis of the variance comparison for the different levels of the factor 'Depth' for macro-benthic organisms associated with Dendrophyllia ramea.

| Depth (m) | Homogeneous groups |
|-----------|--------------------|
| 30 | $***$ |
| 36 | $***$ |
| 42 | $***$ |
| 48 | $***$ |

Dendrophyllia ramea reaches shallower depths in the Atlantic Ocean where, for example, a colony of this species was recorded in the Sagres Caves (Portugal – North Atlantic) at a depth of only 14 m (Boury-Esnault et al., [2001\)](#page-9-0). While in the Mediterranean Sea, its assemblages are mainly distributed below 40 m. In the eastern Basin it is distributed in Greece from 39 m (Salomidi et al., [2010](#page-10-0)), in Turkey 40 m (pers. comm. Dr Mehmet Baki Yokes), in Croatia 43 m (Kružić, [2002](#page-10-0)), in the Ionian Sea at Sicily 70 m (Angiolillo et al., [2022\)](#page-8-0), while in Cyprus it starts at 125 m (Orejas et al., [2017\)](#page-10-0). In the western Basin it is distributed in Nicotera (Italy) at 80 m (Arpacal, [2017](#page-8-0)), reaching up to 173 m in eastern Sardinia (Bonfitto et al., [1994\)](#page-9-0) and up to 161 m in Menorca -Spain (Requena and Gili, [2014\)](#page-10-0).

The Alboran Sea is strongly influenced by the Atlantic Ocean (Candela, [1991](#page-9-0)), where the denser and saltier Mediterranean water mass flows under the Atlantic water mass westward through the Strait of Gibraltar (Bormans et al., [1986\)](#page-9-0). Upon entering the Mediterranean, the Atlantic water masses flow eastward along the northern part of the Alboran Sea (generating the Atlantic Jet) and form two anticyclonic gyres (Western Alboran Gyre and Eastern Alboran Gyre), which reach the southern coast of Morocco (Vargas-Yáñez et al., [2002\)](#page-10-0). The multivariate structure of various species assemblages in the Strait of Gibraltar region, such as opisthobranchs, anthozoans, tunicates and cnidarians, has been observed to possess intermediate characteristics between the Atlantic and central or eastern Mediterranean, potentially extending to the Alboran Sea area (Naranjo, [1995;](#page-10-0) Naranjo et al., [1998;](#page-10-0) Cervera et al., [2004](#page-9-0), González-Duarte et al., [2013\)](#page-9-0). The assemblage of D. ramea in the study area also shows these intermediate bathymetric distribution characteristics, since this area has an average bathymetric distribution between that of the Portuguese and Western Mediterranean populations, reaching depths of between 25 and 30 m at PM (Cebrián et al., [2000;](#page-9-0) Ocaña et al., [2000;](#page-10-0) Cebrián and Ballesteros, [2004\)](#page-9-0), 24 m in Morocco (Salvati et al., [2004](#page-10-0)) and 30 m in Chafarinas Islands (Pers. Obs. González-Duarte). Based on the quantitative sampling of the video transects and multivariate analyses, we distinguished three depth zones defined by the composition and abundance of macro-benthic organisms associated with the D. ramea reef. This variation appears to be primarily driven by the bathymetry of the area, aligning with the depth gradient of the seabed, while additionally being influenced by the presence of *D. ramea*.

Figure 4. Number of species associated with Dendrophyllia ramea reef per depth (m).

CWC are generally associated with other HFS of lower framebuilding potential (Zibrowius, [1980;](#page-11-0) Roberts et al., [2009\)](#page-10-0). This feature produces a high biodiversity in the areas where they are present because they can often be explored by other organisms due to their shelter, nursery or feeding interest (D'Onghia, [2019;](#page-9-0) Otero and Marín, [2019;](#page-10-0) Rueda et al., [2019\)](#page-10-0). Some of these are bryozoans of the species Myriapora truncata and Pentapora fascialis, which are recognised as both primary structure builders (i.e. they build structures alone) or in combination with other organisms, and secondary structure builders. These organisms are important in providing habitat for diverse species and assemblages, playing an important role in promoting biodiversity and habitat heterogeneity (Lombardi et al., [2014](#page-10-0)). Both species characterised the shallowest community (30 m) groups and seem to be conditioned by the availability of hard substrates for settlement.

We have also observed the presence of Parazoanthus axinellae and Axinella damicornis at a depth of 42 m, where they are typically found in a symbiotic relationship with D. ramea as described by Cachet et al. ([2009](#page-9-0)). This association between the cnidarian and sponge species is characteristic of the intermediate depth group studied in the community structure of species at PM,

highlighting the important role of symbiosis in shaping the ecology of marine communities.

As previously mentioned, the result of the PERMANOVA showed that species appear to be conditioned by the availability of rocky substrates. Below 48 m depth, algae are not relevant and suspensivorous organisms become more abundant, such as the sponges Cliona viridis or Haliclona (Reniera) mediterranea. The exception is the invasive alga Rugulopteryx okamurae (E. Y. Dawson) I. K. Hwang, W. J. Lee y H. S. Kim, 2009, which is more abundant at greater depths, probably due to algal downwellings where it is mostly detached from the rocky bottom and dragged by marine currents (Estévez et al., [2022](#page-9-0); Mateo-Ramírez et al., [2023](#page-10-0)).

The present study adds 63 new species and 15 genera to the list of CWC associated fauna of Rueda et al. ([2019](#page-10-0)). The species we identified as most abundant include: Rugulopteryx okamurae (Algae), Crambe crambe and Axinella damicornis (Porifera), Cerianthus membranaceus (Gmelin, 1791) and Parazoanthus axinellae (Cnidaria), Pentapora fascialis and Cellepora pumicosa (Bryozoa), Octopus vulgaris Cuvier, 1797 and Flabellina sp. (Mollusca), Spirobranchus triqueter (Linnaeus, 1758) (Annelida),

Figure 5. nMDS representing the differences in the epibiont community on Dendrophyllia ramea per depth (m). Stress = 0.22.

Table 3. A posteriori pair-wise permutation multivariate analysis of the variance comparison for the different levels of the factor 'Depth' for epibionts growing on Dendrophyllia ramea.

Figure 6. Number of epibiont species on *Dendrophyllia ramea* per depth (m), showing the results of the Generalised Linear Model.

Balanus trigonus Darwin, 1854 (Arthropoda), Arbacia lixula (Linnaeus, 1758) (Echinodermata), Aplidium punctum (Giard, 1873) (Chordata). In the description of the deep-sea communities of the Mediterranean Sea, hydrozoans are a group that are generally not described at the species level and are often grouped together as 'hydroids' (Rueda et al., [2019\)](#page-10-0). This study is one of the few that has identified 15 species of these cnidarians, contributing unique information to previous descriptions of organisms

Table 4. Linear model for the mean average coverage of artificial polymer per depth (m).

SE, standard errors.

For the categorical variable 'Depth', 48 m was used as reference level.

^aMarginally significant. b Significant differences at $P < 0.05$.</sup>

present in the studied ecosystem (Cebrián and Ballesteros, [2004;](#page-9-0) González-Duarte et al., [2013,](#page-9-0) [2014\)](#page-9-0). Among them, Clytia linearis, Campanularia hincksii, Obelia dichotoma, Laomedea sp., Sertularia sp., and Antennella secundaria (Gmelin, 1791) were the most abundant.

In regard to the epibiont community, in the Eastern Mediterranean Sea, bryozoans are the most abundant collected group of epibionts living on the coral D. ramea (Jiménez et al., [2016\)](#page-10-0). In concordance with these results, bryozoans were also the most characteristic epibionts of the coral at all depths studied, particularly the species Cellepora pumicosa. This could be evidence of a close relationship between bryozoans and D. ramea; however, the difficult access to CWC communities limits the extension of our knowledge about their associated species.

Moreover, another significant group of epibionts associated with deep-sea corals in the Mediterranean are the mobile pera-carid species (Cartes et al., [2022\)](#page-9-0). In our study, we identified six different families of peracarids: Caprellidae, Ischyroceridae, Aoridae, Sthenothoidae, Dexaminidae, and Corophiidae. Although we did not find representatives of the Pontogeneiidae family, which is noted to be highly abundant along the coasts of Mallorca in the western Mediterranean, near Punta de la Mona, it is worth mentioning that these findings pertain to much greater depths, exceeding 1000 m (Cartes et al., [2022\)](#page-9-0).

The result of the SIMPER analysis on the epibiont community showed that the shallower depth groups are important as nursery

Figure 7. Average coverage of litter $(cm²)$ for each depth (m) level according to the category.

sites (many recruits and juveniles were observed, including ophiuroids like Ophiothrix fragilis and Ophiura sp., and crabs like Pisidia longicornis and Inachus sp.), including for other HFS such as P. fascialis, especially in the deeper zone (40 and 45 m). The importance of D. ramea as a substrate for many species is reflected in the fact that the number of epibionts increases with depth ([Figure 6\)](#page-7-0), where rocky substrates are less frequent. At 45 m, species like Clytia linearis and Campanularia hincksii seem to contribute significantly to the observed differences, while at shallower depths, species such as Antennella secundaria and Cellepora pumicosa play important roles. In addition, in the deeper zone, corals are largely fractured and wounded due to high anthropogenic impact, especially when compared to the low colony abundance, which also promotes the growth of epibionts on their calcareous skeleton. The combination of both conditions, substrate scarcity and coral injury, explains the increase in the presence of epibionts with depth.

Although D. ramea is a HFS hosting community of native associated organisms (Dayton, [1972\)](#page-9-0), this species also serves as a substrate for non-native species, which can be one of the main threats to biodiversity in marine environments (Galil et al., [2014](#page-9-0)). In the studied population, two non-native species were found as epibionts of D. ramea. One of these was the barnacle Balanus trigonus Darwin, 1854, a species introduced into the Mediterranean Sea, probably before 1850 (Zullo, [1992](#page-11-0)). The other species is the brown seaweed R. okamurae, which could be a risk for the coral due to its highly competitive capacity (Estévez et al., [2022\)](#page-9-0).

Our findings describe how D. ramea colonies are negatively affected by human activity in the PM area, mainly by artisanal fishery, even though it has been listed as a Special Area of Conservation. In particular, fishing lines and ropes may damage or cut coral branches and nets may completely uproot large colonies from the substrate. As a result, urgent action is required to implement a conservation management plan to prevent these detrimental activities in the region. Although marine litter on the seafloor may originate from river discharge (González-Fernández et al., [2021](#page-9-0)) or depend on the hydrodynamic regimen that causes the deposition of plastics and debris in the ocean (Zambianchi et al., [2014](#page-10-0)), fishing line and entagled nets are the results of unregulated fishing activities for this reason, actions are required to implement plans to prevent these detrimental activities.

Other studies have shown that in the Mediterranean Sea, the main types of waste found are, plastics, glass, metal and clinker (Ramirez-Llodra et al., [2013\)](#page-10-0). Among the most abundant types of waste, we have identified debris made of rubber, glass/ceramics, and artificial plastic polymers, with a large number of fishing lines and nets which pluck the branches off the corals. In addition, plastics are of particular importance given they eventually fragment into small particles (microplastics, <5 mm) (Andrady, 2011), which may accumulate in scleractinian corals when mistaken for food particles (Saliu et al., [2019](#page-10-0)), causing coral disease (Nama et al., [2023](#page-10-0)). Furthermore, artificial plastic polymers were found to be more abundant at depths of 36 and 42 m, posing a risk to the D. ramea communities as these depths coincide with the highest coral abundance. The proximity of Marina del Este port suggests it as a primary source of marine debris impacting Punta de la Mona's marine environment. Despite this, there are so far no adequate management plans in the area to prevent waste from reaching the marine environment, although it has long been known that once deposited on the seabed it can modify the surrounding habitat (Saldanha et al., [2003](#page-10-0)). Therefore, the particular and unique coral reef living in PM requires protection given the great anthropogenic impact suffered by the area.

In conclusion, this study emphasises the importance of D. ramea and the necessity of implementing management plans to regulate relevant activities. It provides a quantitative description of the D. ramea assemblage in the Western Mediterranean, on its abundance, distribution patterns, associated biodiversity and the impact from human activities. Notably, the species exhibits higher abundance at shallower depths than typical, which is likely influenced by water mass mixing between the Atlantic Ocean and Mediterranean Sea. Despite the ecological importance of this ecosystem, coral colonies in the study area are under significant threats from fishing and the accumulation of waste and plastics. Urgent conservation management plans are crucial to safeguard this ecologically crucial coral reef and effectively address the negative effects of human impact. Taking prompt action is essential to preserve this valuable coral ecosystem and uphold its vital ecological role in the region.

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Data. All relevant data are included in the manuscript and Supplementary Materials files. The raw data extracted from the videos were used to generate the results and figures. We will consider sharing the videos and images upon request.

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Author Contributions. R. M. E., M. P., L. C. and M. G.-D. conceived the idea and designed the study. M. P. carried out the sampling. R. M. E. and M. G. D. obtained and analysed the data. R. M. E. wrote the first draft of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

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References

- Altuna A and Poliseno A (2019) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals. In Orejas C and Jiménez C (eds), Mediterranean Cold-Water Corals: Past, Present and Future. Cham: Springer, pp. 121–156.
- Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58, 626–639.
- Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253.
- Andrady AL (2011) Microplastics in the marine environment. Marine Pollution Bulletin 62, 1596–1605.
- Angiolillo M, Giusti M, Rossi L and Tunesi L (2022) A Dendrophyllia ramea population in the ionian sea (Central Mediterranean Sea) threatened by anthropogenic impacts. Frontiers in Marine Science 9, 820.
- Arpacal (2017) Colonie di corallo arborescente trovate nella Baia di Nicotera. Available at [https://www.ansa.it/canale_ambiente/notizie/natura/2017/12/](https://www.ansa.it/canale_ambiente/notizie/natura/2017/12/01/colonie-corallo-arborescente-trovate-nella-baia-di-nicotera_ceab1396-e7f3-48de-b02b-28357429d964.html) [01/colonie-corallo-arborescente-trovate-nella-baia-di-nicotera_ceab1396-e7f3-](https://www.ansa.it/canale_ambiente/notizie/natura/2017/12/01/colonie-corallo-arborescente-trovate-nella-baia-di-nicotera_ceab1396-e7f3-48de-b02b-28357429d964.html) [48de-b02b-28357429d964.html](https://www.ansa.it/canale_ambiente/notizie/natura/2017/12/01/colonie-corallo-arborescente-trovate-nella-baia-di-nicotera_ceab1396-e7f3-48de-b02b-28357429d964.html) (Accessed online 23 30 November, 2023).
- Baillon S, Hamel JF, Wareham VE and Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10, 351–356.
- Bianchi CN, Pronzato R, Cattaneo-Vietti R, Benedetti-Cecchi L, Morri C, Pansini M, Chemello R, Milazzo M, Fraschetti S, Terlizzi A, Peirano A, Salvati E, Benzoni F, Calcinai B, Cerrano C and Bavestrello G

(2004) Hard bottoms. In Gambi MC and Dappiano M (eds), Mediterranean Marine Benthos: A Manual of Methods for its Sampling and Study. Monaco: Società Italiana di Biologia Marina (SIMB), p. 604.

Bonfitto A, Bigazzi M, Fellegara I, Impiccini R, Gofas S, Oliverio M, Taviani M and Taviani N (1994) Rapporto scientifico sulla crociera DP 91 (Margine orientale della Sardegna, Mar Mediterraneo). Bollettino Malacologico 30, 129–140.

Bormans M, Garrett C and Thompson KR (1986) Seasonal variability of the surface inflow through the strait of Gibraltar. Oceanologica Acta 9, 403–414.

- Boury-Esnault N, Harmelin JG, Ledoyer M, Saldanha L and Zibrowius H (2001) Peuplement benthique des grottes sous-marines de Sagres (Portugal, Atlantique nord-oriental). In Biscoito M., Almeida A.J., Ré P. (eds) A Tribute to Luiz Saldanha. Boletim do Museu Municipal do Funchal 6, 15–38.
- Bouzinac C, Font J and Johannessen J (2003) Annual cycles of sea level and sea surface temperature in the western Mediterranean Sea. Journal of Geophysical Research 108, 1–20.
- Brito A and Ocaña B (2004) Corales de las Islas Canarias: antozoos con esqueleto de los fondos litorales y profundos. In Lemus F. (ed) Estudios sobre la fauna canaria. Scientia Marina 68, 147–158.
- Brown JH (1995) Macroecology. Chicago and Londres: The University of Chicago Press.
- Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ and Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on deep ocean margins. Marine Ecology 31, 21–50.
- Bulleri F, Eriksson BK, Queirós A, Airoldi L, Arenas F, Arvanitidis C, Bouma TJ, Crowe TP, Davoult D, Guizien K, Iveša L, Jenkins SR, Michalet R, Olabarria C, Procaccini G, Serrão EA, Wahl M and Benedetti-Cecchi L (2018) Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. PLoS Biology 16, e2006852.
- Cachet N, Genta-Jouve G, Regalado EL, Mokrini R, Amade P, Culioli G and Thomas OP (2009) Parazoanthines A−E, hydantoin alkaloids from the Mediterranean Sea Anemone Parazoanthus axinellae. Journal of Natural Products 72, 1612–1615.
- Candela J (1991) The Gibraltar Strait and its role in the dynamics of the Mediterranean Sea. Dynamics of Atmospheres and Oceans 15, 267–299.
- Cartes JE, Díaz-Viñolas D, González-Irusta JM, Serrano A, Mohamed S and Lombarte A (2022) The macrofauna associated to the bamboo coral Isidella elongata: to what extent the impact on Isideidae affects diversification of deep-sea fauna. Coral Reefs 41, 1273–1284.
- Cebrián E and Ballesteros E (2004) Zonation patterns of benthic communities in an upwelling area from the western Mediterranean (La Herradura, Alboran Sea). Scientia Marina 68, 69–84.
- Cebrián E, Ballesteros E and Canals M (2000) Shallow rocky bottom benthic assemblages as calcium carbonate producers in the Alboran Sea, southwestern Mediterranean. Oceanologica Acta 23, 311–322.
- Cervera JL, Calado G, Gavaia C, Malaquias MA, Templado J, Ballesteros MBV, García-Gómez JC and Megina C (2004) An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and archipelagos). Boletín del Instituto Español de Oceanografía 20, 1–122.
- Chevalier JP (1966) Contribución a l'étude des Madréporaires de côtes occidentales de l'Afrique tropicale. Bulletin de l'Institut Fondamental d'Afrique Noire, Série A: Sciences Naturelles 28, 1356–1405.
- Chimienti G, Bo M, Taviani M and Mastrototaro F (2019) Occurrence and biogeography of Mediterranean cold-water corals. In Orejas, C and Jiménez, C (eds), Mediterranean Cold-Water Corals: Past, Present and Future, Vol. 9. Cham, Switzerland: Springer, pp. 213–243.
- Clark MR and Koslow JA (2007) Impacts of fisheries on seamounts. In Pitcher TJ, Morato T, Hart PJB, Clark MR, Haggan N and Santos RS (eds), Seamounts: Ecology, Fisheries, and Conservation. Oxford: Blackwell, pp. 413–441.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.
- Clarke KR and Gorley RN (2006) PRIMER v6: User Manual/Tutorial. Plymouth, UK: PRIMER-E Ltd.
- Clarke KR and Warwick RM (2001) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd Edn. Plymouth: PRIMER-E.
- CoreTeam R (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available at <http://www.R-project.org/> (Accessed 23 November 2023).
- Crain CM and Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. BioScience 56, 211–218.
- Dayton PK (1972) Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In Proceedings of the colloquium on conservation problems in Antarctica. Lawrence, KS, USA: Allen Press, pp. 81–96.
- Díaz JM, Díaz-Pulido G, Garzón-Ferreira J, Geister J, Sánchez J and Zea S (1996) Atlas de los arrecifes coralinos del Caribe colombiano: I. Complejos arrecifales oceánicos. Santa Marta: INVEMAR (Serie de publicaciones especiales No. 2), 83pp.
- D'Onghia G (2019) 30 cold-water corals as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact. In Orejas C and Jiménez C (eds), Mediterranean Cold-Water Corals: Past, Present and Future. Cham: Springer, pp. 335–356.
- Eakin CM, Sweatman HP and Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38, 539–545.
- Echevarría F, Bruno M, Gorsky G, Goutx M, Fernando G, Vargas JM, Picheral M, Striby L, Varela M, Prieto L, Alonso JJ, Reul A, Cózar A, Prieto L, Sarhan T, Plaza F and Jiménez-Gómez F (2002) Physical–biological coupling in the Strait of Gibraltar. Deep-Sea Research II 49, 4115–4130.
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse N L, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B and Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479–486.
- Enrichetti F, Toma M, Bavestrello G, Betti F, Giusti M, Canese S, Moccia D, Quarta G, Calcagnile L, Andaloro F, Greco S and Bo M (2023) Facies created by the yellow coral Dendrophyllia cornigera (Lamarck, 1816): origin, substrate preferences and habitat complexity. Deep Sea Research Part I: Oceanographic Research Papers 195, 104000.
- Estévez RM, Palacios M, Cervera JL and González-Duarte MM (2022) Expansion of the invasive alga Rugulopteryx okamurae (Dictyotaceae, Ochrophyta) in the Mediterranean Sea: first evidence as epiphyte of the cold-water coral Dendrophyllia ramea (Cnidaria: Scleractinia). BioInvasion Recods 11, 925–936.
- Fleet D, Vlachogianni T and Hanke G (2021) A Joint List of Litter Categories for Marine Macrolitter Monitoring. Ispra, Italy: European Commission, Joint Research Centre, EUR 30348 EN.
- Freiwald A, Fossa JH, Grehan A, Koslow T and Roberts JM (2004) Cold-water coral reefs – out of sight no longer out of mind. Biodiversity Series 22. Cambridge, UK: UNEP-WCMC.
- Freiwald A and Roberts JM (eds) (2005) Cold-Water Corals and Ecosystems. Netherland: Springer Science and Business Media, pp.1246.
- Galil BS, Marchini A, Occhipinti-Ambrogi A, Minchin D, Narščius A, Ojaveer H and Olenin S (2014) International arrivals: widespread bioinvasions in European Seas. Ethology Ecology & Evolution 26, 152-171.
- Gómez F, González N, Echevarría F and García CM (2000) Distribution and fluxes of dissolved nutrients in the Strait of Gibraltar and its relationships to microphytoplankton biomass. Estuarine, Coastal and Shelf Science 51, 439–449.
- González-Duarte MM, Megina C and Piraino S (2014) Looking for longterm changes in hydroid assemblages (Cnidaria, Hydrozoa) in Alboran Sea (South-Western Mediterranean): a proposal of a monitoring point for the global warming. Helgoland Marine Research 68, 511–521.
- González-Duarte MM, Megina C, Piraino S and Cervera JL (2013) Hydroid assemblages across the Atlantic–Mediterranean boundary: is the Strait of Gibraltar a marine ecotone? Marine Ecology 34, 33–40.
- González-Fernández D, Cózar A, Hanke G, Viejo J, Morales-Caselles C, Bakiu R, Barceló D, Bessa F, Bruge A, Cabrera M, Castro-Jiménez J, Constant M, Crosti R, Galletti Y, Kideys AE, Machitadze N, Pereira de Brito J, Pogojeva M, Ratola N, Rigueira J, Rojo-Nieto E, Savenko O, Schöneich-Argent R, Siedlewicz G, Suaria G and Tourgeli M (2021) Floating macrolitter leaked from Europe into the ocean. Nature Sustainability 4, 474–483.
- Guzmán HM and Guevara CA (1998) Arrecifes coralinos de Bocas del Toro, Panamá: II. Distribución, estructura y estado de conservación de los arrecifes de las Islas Bastimentos, Solarte, Carenero y Colón. Revista de Biología Tropical 46, 889–912.
- Haapkylä J, Ramade F and Salvat B (2007) Oil pollution on coral reefs: a review of the state of knowledge and management needs. Vie Milieu/Life Environ 57, 91–107.
- Hayes DR, Schroeder K, Poulain PM, Testor P, Mortier L, Bosse A and du Madron X (2019) Review of the circulation and characteristics of intermediate water masses of the Mediterranean: implications for cold-water coral habitats. In Orejas C and Jimenez C (eds), Mediterranean Cold-Water Corals: Past, Present and Future. Cham: Springer, pp. 195–211.
- Hoegh-Guldberg O (2011) Coral reef ecosystems and anthropogenic climate change. Regional Environmental Change 11, 215–227.
- Jiménez CE, Achilleos K, Abu Alhaija R, Gili JM and Orejas C (2016) Living in close quarters: epibionts on Dendrophyllia ramea deep-water corals (Cyprus and Menorca channel). Rapports et Procès-Verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 41, 1.
- Jones CG, Lawton JH and Shachak M (1994) Organisms as ecosystem engineers. Oikos 69, 373–386.
- Kružić P (2002) Marine fauna of the Mljet National Park (Adriatic Sea, Croatia). 1. Anthozoa. Natura Croatica: Periodicum Musei Historiae Naturalis Croaticum 11, 265–292.
- Kružić P, Zibrowius H and Pozar-Domac A (2002) Actiniaria and Scleractinia (Cnidaria, Anthozoa) from the Adriatic Sea (Croatia): first records, confirmed occurrences and significant range extensions of certain species. Italian Journal of Zoology 69, 345-353.
- Lastras G, Sanchez-Vidal A and Canals M (2019) 28 A cold-water coral habitat in La Fonera submarine canyon, northwestern Mediterranean Sea. In Orejas, C and Jiménez, C (eds), Mediterranean Cold-Water Corals: Past, Present and Future, Vol. 9. Cham, Switzerland: Springer, pp. 291–293.
- Lo Iacono C, Savini A, Huvenne VA and Gràcia E (2019) Habitat mapping of cold-water corals in the Mediterranean Sea. In Orejas, C and Jiménez, C (eds), Mediterranean Cold-Water Corals: Past, Present and Future, Vol. 9. Cham, Switzerland: Springer, pp. 157–171.
- Lombardi C, Taylor PD and Cocito S (2014) Bryozoan constructions in a changing Mediterranean Sea. In Goffredo S and Dubinsky Z (eds), The Mediterranean Sea: Its History and Present Challenges. Dordrecht: Springer, pp. 373–384.
- Longo C, Mastrototaro F and Corriero G (2005) Sponge fauna associated with a Mediterranean deep-sea coral bank. Journal of the Marine Biological Association UK 85, 1341–1135.
- Mastrototaro F, D'Onghia G, Corriero G, Matarrese A, Maiorano P, Panetta P, Gherardi M, Longo C, Rosso A, Sciuto F, Sanfilippo R, Gravili C, Boero F, Taviani M and Tursi A (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Part II: topical studies in oceanography. Deep-Sea Research 57, 412–430.
- Mateo-Ramírez Á, Iñiguez C, Fernández-Salas LM, Sánchez-Leal RF, Farias C, Bellanco MJ, Gil J and Rueda JL (2023) Healthy thalli of the invasive seaweed Rugulopteryx okamurae (Phaeophyceae) being massively dragged into deep-sea bottoms by the Mediterranean Outflow Water. Phycologia 62, 99–108.
- McArdle BH and Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.
- Millot C (1992) Are there major differences between the large Mediterranean seas? A preliminary investigation. Bulletin de l'Institut Océanographique, Monaco 11, 3–25.
- Nama S, Shanmughan A, Nayak BB, Bhushan S and Ramteke K (2023) Impacts of marine debris on coral reef ecosystem: a review for conservation and ecological monitoring of the coral reef ecosystem. Marine Pollution Bulletin 189, 114755.
- Naranjo S (1995) Taxonomía, zoogeografía y ecología de las ascidias del Estrecho de Gibraltar (PhD thesis). Universidad de Sevilla, Sevilla, Spain.
- Naranjo S, Carballo JL and García-Gómez J (1998) Towards a knowledge of marine boundaries using ascidians as indicators: characterising transition zones for species distribution along Atlantic-Mediterranean shores. Biological Journal of the Linnean Society 64, 151–177.
- Nykjaer L (2009) Mediterranean sea surface warming 1985–2006. Climate Research 39, 11–17.
- Ocaña A, Tocino LS and González PL (2000) Consideraciones faunística y biogeográficas de los antozoos ('Cnidaria: Anthozoa') de la costa de Granada (Mar de Alborán). Zoologica Baetica 11, 51–66.
- Orejas C, Gori A, Jiménez C, Rivera J, Lo Iacono C, Hadjioannou L, Andreou V and Petrou A (2017) First in situ documentation of a population of the coral Dendrophyllia ramea of Cyprus (Levantine Sea) and evidence of human impacts. Galaxea: Journal of Coral Reef Studies 19, 15–16.
- Otero MDM and Marin P (2019) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement. In Orejas C and Jiménez C (eds), Mediterranean Cold-Water Corals: Past, Present and Future. Cham: Springer, pp. 535–545.
- Patriti G (1970) Catalogue des cnidaires et des cténaires des côtes atlantiques marocaines. Travaux de l'Institut scientifique cherifien et de la Faculté des sciences. Série zoologique 35, 1–149.
- Ramirez-Llodra E, De Mol B, Company JB, Coll M and Sardà F (2013) Effects of natural and anthropogenic processes in the distribution of marine litter in the deep Mediterranean Sea. Progress in Oceanography 118, 273–287.
- Requena S and Gili JM (eds) (2014) Caracterización ecológica del área marina del canal de Menorca: zonas profundas y semiprofundas (100–400 m). Informe final área LIFE+ INDEMARES (LIFE07/NAT/E/000732). Barcelona: Instituto de Ciencias del Mar, Consejo Superior de Investigaciones Científicas (Barcelona). Coordinación: Fundación Biodiversidad.
- Roberts JM, Wheeler A, Freiwald A and Cairns S (2009) Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats. New York: Cambridge University Press, 334pp.
- Rueda JL, Urra J, Aguilar R, Angeletti L, Bo M, García-Ruiz C and Taviani M (2019) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas. In Orejas C and Jiménez C (eds), Mediterranean Cold-Water Corals: Past, Present and Future. Cham: Springer, pp. 295–333.
- Saldanha HJ, Sancho G, Santos MN, Puente E, Gaspar MB, Bilbao A and Arregi L (2003) The use of biofouling for ageing lost nets: a case study. Fisheries Research 64, 141–150.
- Saliu F, Montano S, Leoni B, Lasagni M and Galli P (2019) Microplastics as a threat to coral reef environments: detection of phthalate esters in neuston and scleractinian corals from the Faafu Atoll, Maldives. Marine Pollution Bulletin 142, 234–241.
- Salomidi M, Zibrowius H, Issaris Y and Milionis K (2010) Dendrophyllia in Greek waters, Mediterranean Sea, with the first record of D. ramea (Cnidaria, Scleractinia) from the area. Mediterranean Marine Science 11, 189–194.
- Salvati E, Giusti M, Canese S, Esposito V, Romeo T, Andaloro F, Bo M and Tunesi L (2021) New contribution on the distribution and ecology of Dendrophyllia ramea (Linnaeus, 1758): abundance hotspots off northeastern Sicilian waters. Aquatic Conservation: Marine and Freshwater Ecosystems 31, 1322–1333.
- Salvati E, Tunesi L and Molinari A (2004) Presence of the Scleractinian Dendrophyllia ramea in the shallow waters of Mediterranean Morocco (Al Hoceima, Alboran Sea). Rapports et Procès-Verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 37, 547.
- Sánchez P, Demestre M and Martın P (2004) Characterisation of the discards generated by bottom trawling in the northwestern Mediterranean. Fisheries Research 67, 71–80.
- Sarhan T, Lafuente JG, Vargas M and Plaza F (2000) Upwelling mechanisms in the northwestern Alboran Sea. Journal of Marine Systems 23, 317–331.
- Skliris N and Beckers JM (2009) Modelling the Gibraltar Strait/Western Alboran Sea ecohydrodynamics. Ocean Dynamics 59, 489–508.
- Stachowicz J (2001) Mutualism, facilitation, and the structure of ecological communities. BioScience 51, 235–246.
- Vargas-Yáñez M, Plaza F, García-Lafuente J, Sarhan T, Vargas JM and Vélez-Belchi P (2002) About the seasonal variability of the Alboran Sea circulation. Journal of Marine Systems 35, 229–248.
- Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. New York: Springer, Use R! Series, 213pp.
- Wildish D and Kristmanson D (1997) Benthic suspension feeders and flow. Cambridge University Press, Cambridge, UK. Zibrowius H. 1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mémoires de l'Institut océanographique, Fondation Albert 1er, Prince de Monaco 11, 169–172.
- Zambianchi E, Iermano I, Suaria G and Aliani S (2014) Marine litter in the Mediterranean Sea: an oceanographic perspective. In Briand, F (ed), Marine

Litter in the Mediterranean and Black Sea, Vol. 46. Monaco: CIESM Publishers, pp. 31–41.

- Zibrowius H (1980) Les scléractiniaires de la méditerranée et de l'Atlantique nord-oriental. Mémoires de l'Institut océanographique, Fondation Albert 1er, Prince de Monaco 11, 169–172.
- Zibrowius H (1981) Scléractiniaires récoltés par R. Ph. Dollfus sur la côte atlantiquedu Maroc (campagnes du 'Vanneau' 1923–1926). Bulletin de l'Institut Scientifique, Rabat 5, 1–12.
- Zullo VA (1992) Balanus trigonus Darwin (Cirripedia, Balaninae) in the Atlantic basin: an introduced species? Bulletin of Marine Science 50, 66–74.