



## From emblematic to problematic: The case of *Astrospartus mediterraneus* (Risso, 1826) (Echinodermata: Ophiuroidea) in the artisanal fishing grounds of the Cap de Creus area (NW Mediterranean Sea)

Marina Biel-Cabanelas<sup>a,b,\*</sup>, Andreu Santín<sup>a</sup>, Mireia Montasell<sup>a</sup>, Janire Salazar<sup>a</sup>, Patricia Baena<sup>a</sup>, Núria Viladrich<sup>c,d</sup>, Maria Montseny<sup>e</sup>, Guillem Corbera<sup>f</sup>, Stefano Ambroso<sup>a</sup>, Jordi Grinyó<sup>a,g</sup>

<sup>a</sup> Institut de Ciències Del Mar (ICM-CSIC), Barcelona, Spain

<sup>b</sup> Program in Biodiversity, Universitat Autònoma de Barcelona, Bellaterra 08193, Barcelona, Spain

<sup>c</sup> School of Aquatic and Fishery Sciences, University of Washington, Seattle, 98105, Washington State, USA

<sup>d</sup> Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain

<sup>e</sup> Departamento de Zoología, Universidad de Sevilla, Sevilla, Spain

<sup>f</sup> Departament de Dinàmica de la Terra i l'Oceà, Universitat de Barcelona, Barcelona, Spain

<sup>g</sup> Department of Ocean System Sciences, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, Den Burg, the Netherlands

### ARTICLE INFO

#### Keywords:

Artisanal fishing  
Local ecological knowledge  
Remoted operated vehicles  
Ophiuroid blooms  
Gorgonacephalidae  
By-catch

### ABSTRACT

Although *Astrospartus mediterraneus* (Risso, 1826) is an emblematic Mediterranean species, limited information is currently available, as it has not received much attention from the marine scientific community to date. In this context, an unusually high abundance of this basket star was observed in 2018 as part of the by-catch of local artisanal fishers in the Cap de Creus area (NW Mediterranean Sea). Indeed, fishers reported that this species had increased in abundance and expanded its distribution in recent years, ultimately interfering with their fishing activity. As such, this study aimed to elucidate the abundance, distribution, size, and structure of *A. mediterraneus* populations, as well as to evaluate the potential impact this species has on artisanal fisheries' performance in the study area. To such aim, this work benefited from the Local Ecological Knowledge (LEK) of the fishers, by-catch analyses of regular fishing events and video transects recorded employing Remote Operated Vehicles (ROV).

Results show that *A. mediterraneus* has a specific distribution in the study area, mainly driven by habitat requirements. High abundances of the basket star were associated with rocky substrates with the presence of gorgonians, located between 50 and 80 m depth and preferentially occurring on sloping areas. Despite the lack of long-time monitoring data, *A. mediterraneus*' aggregations recorded in the studied area are the densest ones so far reported for the whole Mediterranean Sea with peak values of 18 ind. m<sup>-2</sup> and a mean density of 0.45 ind. m<sup>-2</sup> ± 0.71 ind. m<sup>-2</sup>. Additionally, the average size of their central disks (2.67 ± 0.97 cm), suggests that this is rather young population, which could be possibly linked with the beginning of a massive outbreak, which would be in accordance with the fishers' own experiences, as it seems apparent that the species has been on the rise in recent years. Furthermore, they unanimously consider this proliferation to be a considerable handicap in terms of time and monetary losses.

Overall, additional studies are needed to increase current knowledge on the ecology of this species. Understanding the species will be paramount to monitor and assess this phenomenon with stakeholders to avoid further ecological and economic consequences.

### 1. Introduction

Certain suspension-feeder ophiuroids can occasionally occur in

notably high abundances, forming brittle star or ophiuroid seabeds (Warner and Woodley, 1975; Metaxas and Giffin, 2004; Domínguez-Carrió et al., 2022). These formations are composed of hundreds

\* Corresponding author. Institut de Ciències Del Mar (ICM-CSIC), Barcelona, Spain.

E-mail address: [marinabel@icm.csic.es](mailto:marinabel@icm.csic.es) (M. Biel-Cabanelas).

<https://doi.org/10.1016/j.csr.2023.104925>

Received 27 October 2022; Received in revised form 23 December 2022; Accepted 7 January 2023

Available online 21 January 2023

0278-4343/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

(Blaber et al., 1987) to thousands of individuals, sometimes exceeding 2,000 individuals per m<sup>2</sup> (Allen, 1998). Due to the high biomass they encompass, such ophiuroid beds demand a large share of carbon (Metaxas and Giffin, 2004) and are believed to be important calcite (CaCO<sub>3</sub>) reservoirs (Migné et al., 1998; Ellis and Rogers, 2000; Ruhl, 2007), thus becoming a major component of the carbon cycle (Aronson, 1992; Metaxas and Giffin, 2004). Ophiuroid aggregations generally occur in shallow waters up to 15 m (Warner and Woodley, 1975; Calero et al., 2018), although they have also been observed at hundreds of meters depth (i.e., 450 m on the continental slope, Blaber et al., 1987). Currently, there is no concrete explanation as to why these massive aggregations occur (Uthicke et al., 2009), and the mechanisms triggering this increment in abundance generally remain unknown. However, it has been suggested that they may be related to feeding requirements (Warner and Woodley, 1975) or an amelioration of the environmental setting through the presence of assemblages of branching sessile suspension feeders (e.g. octocorals or sponges) (Calero et al., 2018).

Within suspension-feeding ophiuroids, basket stars (Gorgonocephalidae family) present a worldwide distribution, with occurrences reported from shallow subtidal areas to the deep sea (Clark, 1911; Patent, 1970a), yet, fundamental aspects of their biology remain to be described (Davis, 1966; Escoubet et al., 2001; Rosenberg et al., 2005). The basket stars' body plan displays a pentagonal-to-round central disc from which five multibranching arms emerge. Besides being used for feeding, the arms are a valuable part of the animal's locomotion (Emson et al., 1991; Patent, 1970a; Rosenberg et al., 2005; Stöhr et al., 2012). Movement is carried out by twisting and coiling their arms, pushing them against a surface, or gripping objects to pull themselves forward (Stöhr et al., 2012). These organisms generally display nocturnal feeding habits (Warner, 1982; Harris et al., 2009; Blanchet-Aurigny, 2012), mainly preying on zooplankton (e.g. fish and crustacean larvae, copepods, appendicularians) and/or capturing suspended particulate organic matter (Mortensen, 1923; Davis, 1966; Allen, 1998). To maximize the capture of suspended particles and prey, they have been described to ascend to the nearest prominence, often climbing onto benthic structural elements (e.g. rocks, sessile fauna) or non-natural elements protruding from the seabed (e.g. fishing gear). They then proceed to spread their multibranching arms, oriented toward the current, to become an effective trap to entangle their prey (Davis, 1966; Stöhr et al., 2012). As prey encounter is occasional (Emson et al., 1991), these organisms can maintain a feeding posture with arms bending against the current for long periods of time (Rosenberg et al., 2005). Indeed, basket stars are known to be typically associated with rocky substrates (Gondim et al., 2015) and key benthic structural organisms such as some anthozoans or sponges (Davis, 1966; O'Hara, 2007).

The basket star *Astrospartus mediterraneus* (Risso, 1826) is the sole representative of the Gorgonocephalidae family in the Mediterranean Sea (Ocaña and Pérez-Ruzafa, 2004), with its distribution spreading from the eastern North Atlantic coasts of Africa and Europe to the Mediterranean Sea (Zibrowius, 1978). The species is considered a rare and emblematic species (Escoubet et al., 2001; Mallol, 2010; Santín et al., 2022) and in need of conservation and protection (Cocito et al., 2015; Fitori et al., 2022). Yet, there is almost no information regarding its biology or ecology (Zibrowius, 1978; Escoubet et al., 2001).

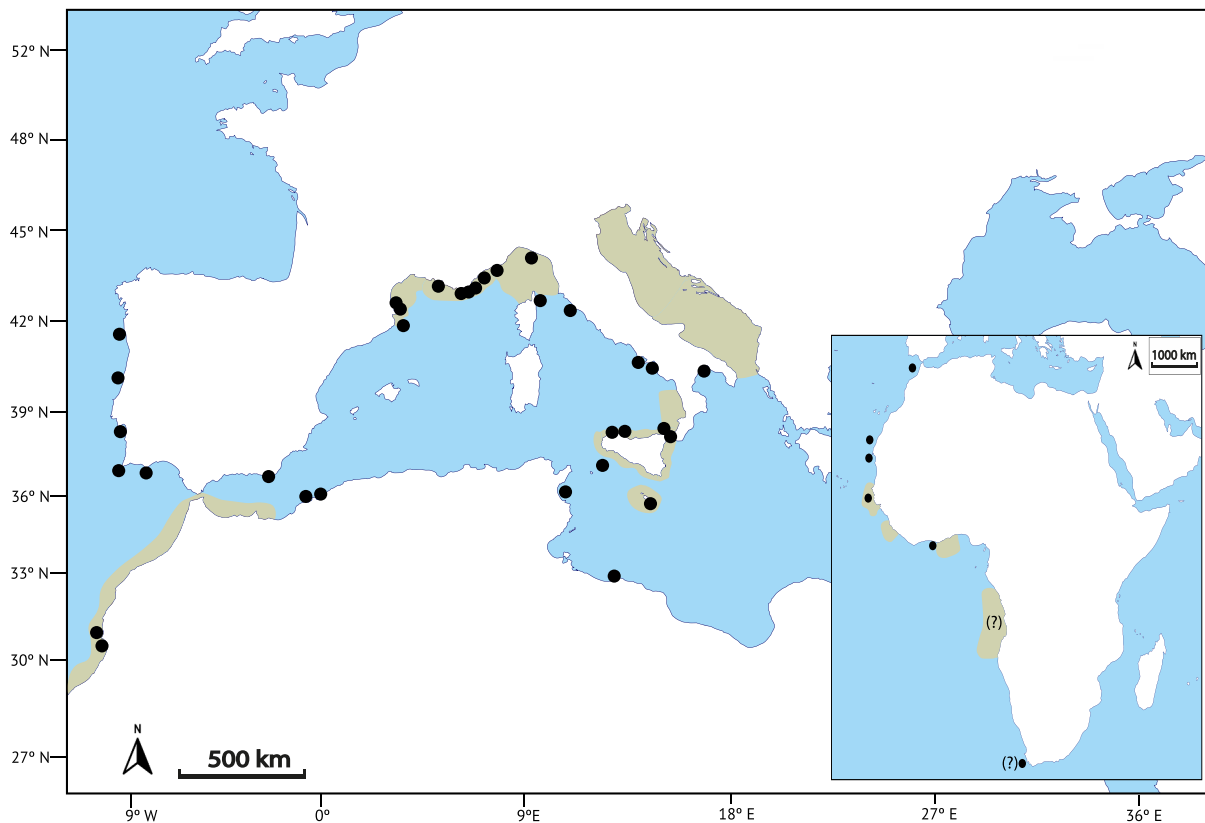
*Astrospartus mediterraneus* displays a grayish coloration and its ventral side is embroidered by small, yellowish regular dotted lines (Risso, 1826; Koehler, 1921). Despite its occurrence over a wide geographic and bathymetric range — 30 to 240 m depth — (Zibrowius, 1978; Leonard et al., 2020), the species has been mostly overlooked by the scientific community for years, with a relatively small quantity of reports since it was first described, most of which lacked any specifications in regard to an exact location, depth, or number of individuals found (e.g. Chella Seamount, Lo Iacono et al., 2012; Palamós Submarine Canyon, Lastras et al., 2016; Cap de Creus, Gili et al., 2011, Table 1. Supplementary material). Nevertheless, in recent years an unusually

high number of individuals has been noticed to occur within the Cap de Creus marine area (northwest Mediterranean Sea) by local fishermen (Santín et al., 2022). This area holds some of the most diverse benthic communities in the Catalan margin (Gili et al., 2011; Lo Iacono et al., 2012; Madurell et al., 2012; Domínguez-Carrió et al., 2022), and includes both the Special Area of Conservation (SAC) of the Cap de Creus (CdC) Natural Park (ES5120007) and the Site of Community Importance (SCI) of the “Sistema de cañones submarinos occidentales del Golfo de León” (ESZZ16001). Since the founding of the Cap de Creus (CdC) Natural Park in 1998 numerous ecological studies have been conducted in the area, being considered as one of the most well-known areas on the Catalan coast (Gili et al., 2011). In this sense, within the natural park and the SCI boundaries the presence of *A. mediterraneus* had been known about for decades, yet records were rare and usually corresponded to few or isolated individuals (Fig. 1. Table 1. Supplementary material.)

Within the CdC Natural Park area and limits, fishing is strongly regulated and restricted to small-scale artisanal fisheries conducted on vessels between 6 and 9 m in length, with a crew of up to two people working near the shore, closer than a nautical mile, and using different static gears depending on the targeted species (Gómez and Lloret, 2016; Lloret et al., 2018). While sometimes neglected, over the course of the years artisanal fishers gather an extensive amount of information on the ecology of local species, the functioning of marine systems, and the sea's environmental conditions (Johannes, 1984; Sardà and Maynou, 1998). As an example, they have become acquainted with the migrations, habitats, spawning time and grounds (Johannes, 1981; Neis et al., 1999), feeding areas (Hamilton and Walter, 1999), nursery areas (Johannes and Ogburn, 1999) and reproduction periods of many species (Johannes, 1984, 1998). Furthermore, their daily interaction with marine species results to be, in several cases, the only available source of information on changes in local ecosystems (Paterson, 2010). The integration and accumulation of a body of knowledge, understandings, beliefs, and practices that human societies develop in relationship with their natural environment is known as Local Ecological Knowledge (LEK) (Berkes et al., 2000; Aswani et al., 2018). In the fishers' case, their LEK has proven to help assess the abundance of benthic resources (Garmendia et al., 2021) and provide valuable information about both commercial and non-commercial species (Paterson, 2010). Fishers' LEK may potentially improve fishery and local biodiversity management, by providing new data about the ecology, behavior, and abundance of species, local ecological processes and their influences on fishing resources.

In this context, in 2018, within the framework of the MITICAP Project (*Implementación de medidas innovadoras de cooperación entre pescadores y científicos para una mejor gestión de la pesca artesanal con el objetivo de mitigar sus impactos en hábitats marinos sensibles*), fishers from the guilds of Port de la Selva and Cadaqués, which mainly work within the limits of the CdC Natural Park, stated that they noticed a substantial increase in the abundance of *A. mediterraneus* over the past five years. After assessing the fishing by-catch generated by different gears, it was evident that, indeed, *A. mediterraneus* represented a large proportion of total catches (Santín et al., 2022), and such situation had begun to be perceived as a problem by fishers from both guilds.

The considerable knowledge gap regarding the ecology of *A. mediterraneus*, combined with the fishers' concern about its perceived massive population increase and associated detrimental effects, has raised a flag on this matter. Yet the context of a collaborative project involving marine researchers and fishers has provided an opportunity to investigate the issue further. As such, the present study aims to gain insight into the ecology of *A. mediterraneus*' populations and determine their potential effects on artisanal fishers' performance by specifically: i) Identifying the ecological requirements of *A. mediterraneus*, to comprehend its distribution, abundance and CdC population structure; and ii) examining its interaction with local fishers to understand whether they have an impact on each other and analyze the socioeconomic impact of the occurrence of *A. mediterraneus*.



**Fig. 1.** *Astrospartus mediterraneus* presence in the Atlanto-Mediterranean region registered from 1556 to 2022. Black dots indicate specific locations cited in the reviewed literature, whereas beige areas represent registers with inaccurate or generic indications on the species' location. Locations marked with (?) correspond to probable misidentification. See Table 1 in Supplementary material for further information regarding each location.

## 2. Materials and methods

### 2.1. Study area

The CdC area (42°19'12" N, 03°19'34" E) located in the north-western region of the Mediterranean Sea (Fig. 2) is the most westerly point of the Gulf of Lions. The continental shelf off the cape is incised by the CdC submarine canyon system. Both the shelf and the canyon comprehend an ample range of ecosystems and include spots that shelter representatives of almost every type of the typical Mediterranean benthic communities (Madurell et al., 2012; Sardà and Company, 2012). Indeed, this area was declared a maritime-terrestrial Natural Park in 1998 (Law 4/1998 (Official State Gazette [BOE], 1998)) and a Special Protection Area (SPA) in 2014 (Area ES5120007 of the Natura 2000 Network (Order AAA/1299/2014 (BOE, 2014))) also adjacent to a Site of Community Importance (SCI) of the protected areas of the European Union (Area ESZZ16001 (BOE, 2014)).

This study was conducted on the fishing grounds shared by both collaborating guilds (Cadaqués and Port de la Selva) which mostly operate on the north side of the CdC. These fishing grounds are characterized by their complex bathymetry, with high slopes and rocky bottoms (Gori et al., 2012; Sardà and Company, 2012). Water temperature in the area oscillates from 10.1 to 24.3 °C at 20 m depth, and 10.7–21.1 °C at 60 m depth throughout the year (Gori et al., 2012). The general water circulation is driven by the Northern current, which promotes a northeast to southwest water flow (DeGeest et al., 2008). The primary source of hemipelagic sediments in the study area comes from the Rhône river (DeGeest et al., 2008; Ulses et al., 2008), with up to 80–90% of the continental shelf's sediments being provided by this river (Courp and Monaco, 1990). Northern winds (Tramontane and Mistral) are the dominant winds in the area. Persistent, cold, and dry, its characteristics provoke water mixing and the densification of coastal waters,

leading to coastal downwelling in the study area (Ulses et al., 2008).

### 2.2. Fishing events

Members of the research team joined the artisanal fishers' fleet from the Port de la Selva and Cadaqués guilds (Catalonia, Spain) during regular fishing events, defined as a daily fishing activity using a certain type of gear. In total, nine fishing vessels were involved, six of them harbored in Port de la Selva and three in Cadaqués. Altogether, 143 fishing events, occurred 118 in Port de la Selva and 25 in Cadaqués. The fishing events took place from April to August of 2018, during the spiny lobster (*Palinurus elephas* (Fabricius, 1787)) and scorpion fish (*Scorpaena scrofa* (Linnaeus, 1758)) fishing season, and combine it with *Octopus vulgaris* (Cuvier, 1797) fishing. Different fishing gears were used and checked for *A. mediterraneus* by-catch, such as: i) pots, cages and baskets made from various materials and with one or more openings; ii) trammel nets, consisting of three layers of netting, a small and slacker mesh in between two larger ones; and iii) "solta", gillnets, with a single mesh (Nédélec and Prado, 1990). The nets were kept vertical by floats on the headrope and weights on the ground rope, whereas the pots were set on the bottom, baited or empty, and connected by ropes to buoys on the surface. For each fishing event, data about sea conditions, type of gear used, setting and collection hour and day, depth, and coordinates were gathered (Montseny et al., 2019). *A. mediterraneus* caught in fishing gear were carefully untangled and then photographed *in situ* using camera devices with a minimum resolution of 16 megapixels. Each picture was taken with a graduated grid in centimetric units, which was used for scaling purposes (Fig. 3). After measuring, sampled individuals were returned back to the sea.

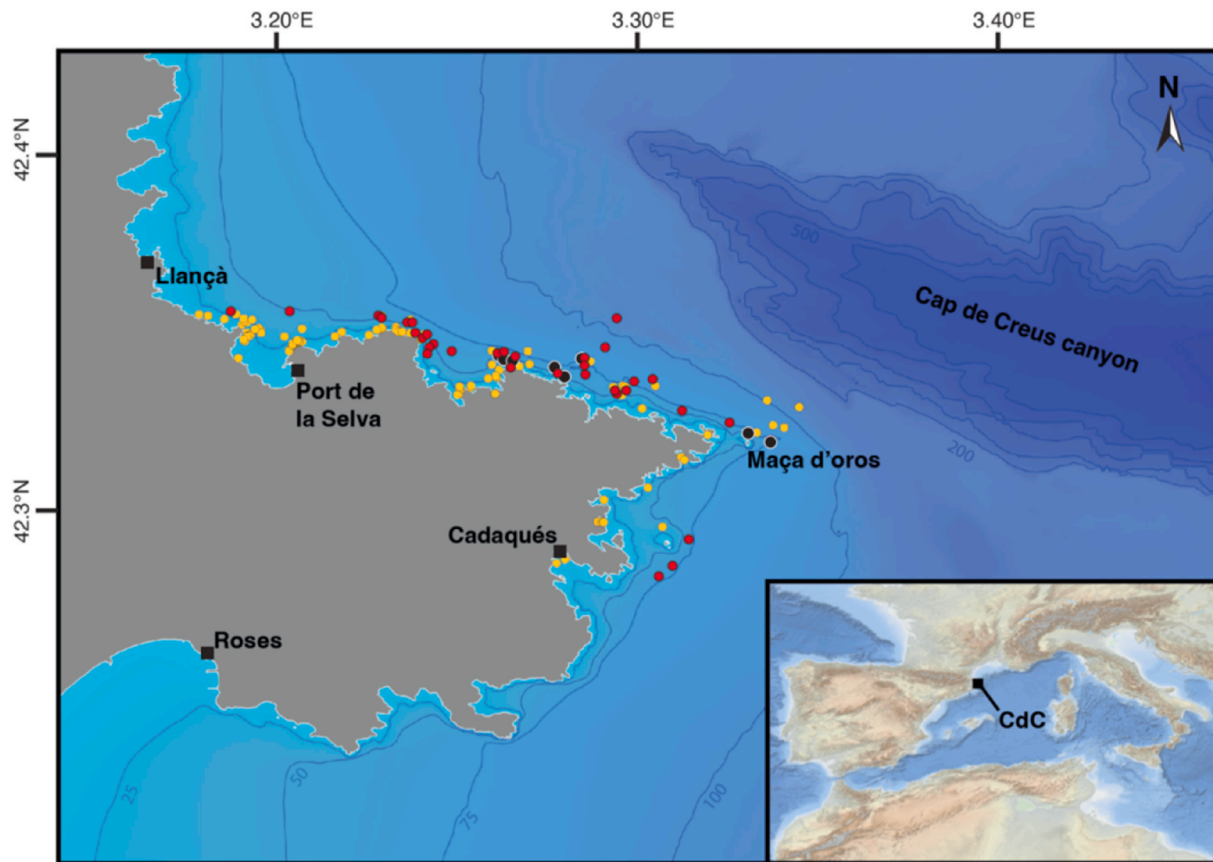


Fig. 2. Cap de Creus marine area. The red and yellow circles indicate the fishing stations with *Astrospartus mediterraneus* presence or absence, respectively. The location of remotely operated vehicle (ROV) video transects are remarked in black circles. Projected view UTM Zone 31N (WGS84) with geographic (WGS84) coordinates indicated for reference.

### 2.3. Morphological analyses and size-frequency distribution

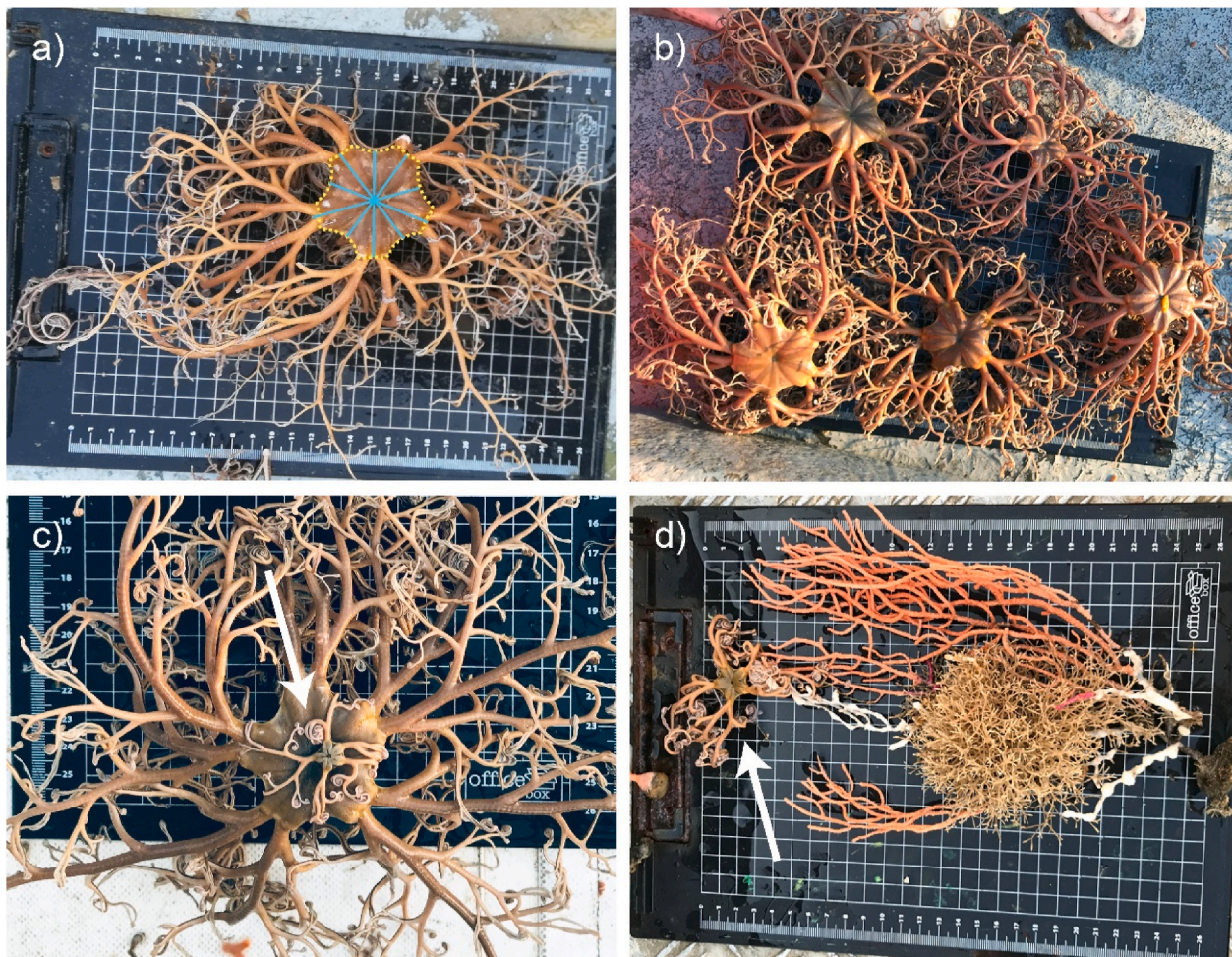
Photometric analyses were carried out with Magnification v.1.8 software (Orbicule) by taking several morphometric measurements of the central disc (diameter, perimeter, and area) per individual from by-catch pictures (Fig. 3a). Diameter values were acquired as an average of measuring each individual five times from the start of each arm to the opposite side. A total of 418 individuals were analyzed, with their mean diameter, perimeter, and area used to perform the morphological analyses. For data analysis, all tests and functions mentioned below were performed using the R software v4.1.1. (R Core Team, 2021). A Pearson correlation test was performed between diameter and perimeter, using the *cor.test* function to determine if the variables correlated assess which could be most suitable for subsequent analyses. To graphically represent the size-distribution frequency of *A. mediterraneus*, histograms were generated for each fishing event by grouping the individuals by disc diameter (categories: 0–1 cm, 1–2 cm, 2–3 cm, 3–4 cm, 5–6 cm, and 6+ cm; Fig. 4) employing the *fdth* package (Faria et al., 2016). Secondly, to assess the size structure of the by-caught individuals, different *A. mediterraneus* clusters were evaluated. Every fishing station in which it was by-caught in numbers equal or higher to 10 was considered as a single aggregation, for a total of 10 aggregations evaluated. The skewness and kurtosis for each suitable fishing event were calculated through the use of the *agostino.test* (Komsta and Novomestky, 2012) and *anscombe.test* (Anscombe and Glynn, 1983) respectively, both part of the *moments* package (Komsta and Novomestky, 2012). Skewness is a measure that evaluates the symmetry of a distribution based on its mean value (Linares et al., 2008). If the *p-value* is < 0.05, data distribution is asymmetric. If skewness values are positive, data show a dominance of small-size organisms, but if they are negative values, large organisms

prevail in the fishing event distribution. Kurtosis measures the peakedness of distribution near its central model (Linares et al., 2008). So, if the *p-value* is < 0.05, there is a prevalence of a specific size in each fishing event. Only fishing events with 10 or more individuals were considered suitable for skewness and kurtosis tests, as lower values could compromise the analyses.

### 2.4. Video recording and video analyses

To characterize the artisanal fishing grounds in the Cap de Creus area, a total of 19 video transects were recorded onboard the vessel 'Atlantic Explorer' using the Perseo ROV (Fig. 2). The latter was equipped with a high-definition (HD) camera, with an additional 4K camera that was used in only 11 video transects, depth sensors, and two parallel laser beams 30 cm apart that provided a fixed scale. The ROV monitoring took place from the 25th to the 30th of July 2018. Transect length ranged from 174.03 to 1154.66 m, covering a total of 9 km, whereas transect depth varied from 11.5 to 80 m water depth.

Each transect was divided into 2 m<sup>2</sup> sampling units (0.3 m width and 6.66 m length), based on the minimal sampling area suggested by Weinberg (1978), who estimated 2 m<sup>2</sup> to be an area large enough for the study of benthic communities in the rocky bottoms of the Mediterranean Sea. This approach has subsequently been used by other studies in this basin (Ambroso et al., 2013; Grinyó et al., 2016; Corbera et al., 2019). Analyses were carried out with Final Cut Pro 7 video processing software (Apple Inc., 2009). The transect onset was established once the ROV was positioned over the seabed and started moving with a consistent heading. For every individual *A. mediterraneus* observed during the transect, the following information was compiled: depth, associated substrate type (including epiphyted organisms, if any), and the geographical



**Fig. 3.** By-catch *Astrospartus mediterraneus* individuals, obtained from the fishing gear of artisanal fishers, with a scaled grid as a background for scale. **a)** Indication of the *A. mediterraneus* measures taken for photo analyses. Blue lines correspond to diameter measurements, and the yellow dotted line to perimeter measurements. **b)** Five individuals by-caught by trammel nets. **c)** Adult exemplar of *A. mediterraneus* with a small, younger individual attached to its disk. **d)** *Eunicella cavolini* colony with an *A. mediterraneus* individual entangled in its branches.

coordinates. Moreover, substrate type and slope were also registered for each sampling unit, following the categories in Santín et al. (2018). Sequences not suitable for posterior video analysis (e.g. with suspended sediment or too far away from the seafloor) were discarded. Transect velocity ( $v$ ) was calculated by dividing the transect distance (m) by its duration (t). Time references were posteriorly transformed into a known position ( $P = t \cdot v$ ), where (P) is the position, (t) is the time at which every individual was found, and (v) the velocity of the ROV. For data analysis, all tests and functions mentioned below were performed using the R software v4.1.1. (R Core Team, 2021).

### 2.5. Geographical and bathymetrical distribution

The geographical distribution of *A. mediterraneus* was carried out plotting the density (video) and abundance (fishing events) values on georeferenced maps using the *raster* (Hijman, 2016), *sp* (Bivand et al., 2013), and *rgdal* (Bivand et al., 2017) packages. To assess *A. mediterraneus*' bathymetrical distribution, boxplots and bagplots were generated for each species' density values and for each depth interval, using the *aplpack* package (Wolf, 2019).

### 2.6. Environmental factors influencing its distribution

To better understand and illustrate the possible relation between *A. mediterraneus* populations and their surrounding environmental

factors, values from the video analysis were grouped by a series of factors, as follows: 1) depth (10–30 m, 30–50 m, 50–70 m, 70–90 m); 2) substrate (soft sediments, cobbles and pebbles, rock); 3) slope (horizontal, sloping, vertical); 4) density of Derelict Fishing Gear (DFG, represented as  $DFGs.m^{-2}$ ); and 5) principal Ecosystem Engineers (ENs): i) soft corals (*Alcyonium* spp.) and pennatulacean communities, *Pennatula* spp. and *Pteroeides griseum* (Bohadsch, 1761); ii) gorgonian forests (*Eunicella* spp.); and iii) barren rocky grounds. Several scatterplots were produced using these variables, employing the *ggplot2* package (Wickham, 2016). Data were also tested for statistical differences between categories on each of the aforementioned groups. Prior to analysis, normality and homogeneity tests were conducted through the *shapiro.test* (González-Estrada et al., 2013) and *barlett.test* (Savchev et al., 2018) functions, available as part of the basic *stats* package. An ANOVA test was performed using the *aov* function of the *stats* package to test for possible differences between groups. If the ANOVA tested to be statistically significant, a *posthoc* analysis was performed utilizing the *pairwise.t.test* of the *stats* package to elucidate differences amongst specific groups.

### 2.7. Fishers' perception and experience with *A. mediterraneus*

To estimate the impact of a possible basket star outbreak, fishers completed a survey regarding this issue (see Supplementary material 2). Prior to each survey, an individual consent form was signed by each

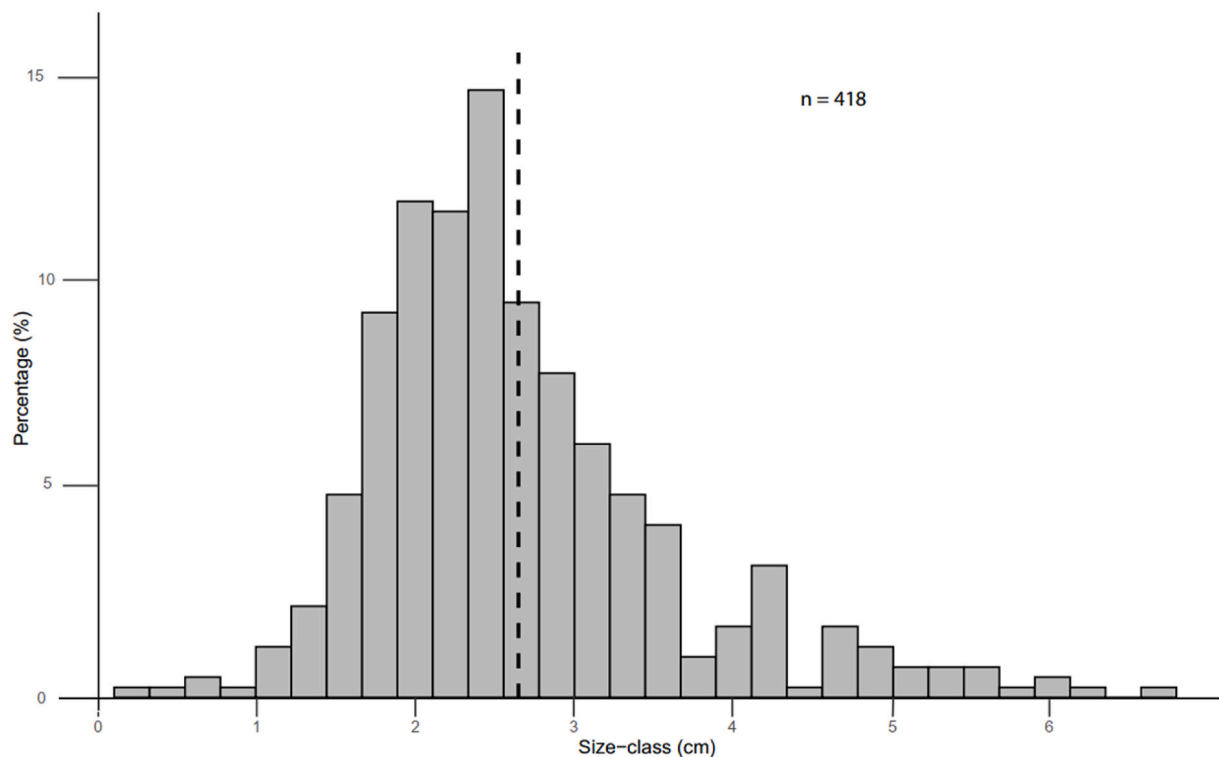


Fig. 4. Size-frequency distribution of *A. mediterraneus* by-caught in artisanal fishing during the 2018 spiny lobster and scorpion fish fishing season (April to August). The number of individuals analyzed are shown as (n). The black dotted line determines the mean disk diameter size of all the individuals collected.

fisher, formally stating that they accepted to be interviewed and informing them about the use and protection of their data, under the Spanish decree-law (*Ley Orgánica*) 3/2018 (BOE, 2018). All the fishers from the collaborating guilds answered the survey, but it was also extended to other fishing guilds in Catalonia to better determine if this phenomenon was of local or regional scope. The selection criteria to take the survey were: (i) being an active artisanal fisher; (ii) being located on the Catalan coast. The participating guilds were divided by regions: North (Port de la Selva, Cadaqués, Roses); Central (Vilanova i la Geltrú, Sant Feliu de Guíxols, Blanes, Arenys de Mar); and South (La Ràpita, Sant Joan de Deltebre). The survey was composed of 22 questions regarding their fishing history, gear used, outgoing frequency, recognition of an exemplar of *A. mediterraneus*, catch history of the studied species, and their personal perception of the issue (Supplementary material 2). The questionnaire aimed to assess the collective's insight about the *A. mediterraneus*' population tendencies, discern whether it has an impact on their daily work, and determine to what extent it affected them. Questionnaires were collected between the 18th and 19th of September 2021, during an Artisanal Fishing Congress held at Lloret de Mar (Catalonia, Spain), where both online and in-person attendance options were available.

### 3. Results

#### 3.1. Size-distribution frequency and morphology

A high correlation ( $R^2 = 0.92$ ,  $p$ -value = < 0.001) was found between the morphometric variables diameter and perimeter. Therefore, diameter was preferred over perimeter to perform the histograms for the size-frequency distribution of each aggregation (Fig. 4) due to the possibility of taking several measures per individual and calculating the mean value. The average diameter size was  $2.67 \pm 0.97$  cm, ranging between 0.19 and 6.67 cm. Most aggregations from cluster analyses showed 49.04% of individuals with a size-frequency of between 2 and 3 cm, followed by classes of 1–2 cm (22.48%) and 3–4 cm (17.46%) (Fig. 4).

Size classes comprising between 4 and 6 cm represented percentages lower than 10%, whereas the 0–1 cm and over 6 cm size classes represented less than 5% for all aggregations. Size-distribution presents an asymmetric distribution ( $p$ -value = < 0.001) in terms of skewness test; with a dominance of small- and medium-size classes (1–5 cm). Moreover, kurtosis test showed a significant peakedness ( $p$ -value = < 0.001) with a clear size prevalence of 2–3 cm individuals (Table 1; Supplementary material 2).

#### 3.2. Geographic and bathymetrical distribution

Results from by-catch show a similarly abundant tendency over the study area (Fig. 5a.), with an average of  $6.36 \pm 22.44$  individuals per fishing cast but increasing to  $15.96 \pm 33.49$  individuals when considering only trammel nets. However, the maximum number of individuals found was 150. Even so, the greatest abundances (over 100 individuals) occurred in just four events among 143 totals analyzed, spread along the entire sampled area (Fig. 5a). Density maps developed from video transects found the mean density to be  $0.45 \pm 0.71$  ind.m<sup>-2</sup> and the largest densities of the species to be at the northwest flank of the study area (Fig. 5b). Further, it revealed two main aggregation zones: one in the central part of the north CdC coast, close to the fishing grounds of Port de la Selva, where most of the fishing events occurred (Fig. 2), and the second one close to Massa d'Or, where abundances of over 75 individuals in some fishing events were recorded (Fig. 5a).

Both data from video analyses and fishing events showed a similar bathymetrical distribution for the species, with an overall distribution between 35 and 85 m, but with a high incidence of *A. mediterraneus* restricted between 50 and 80 m depth (Fig. 6). Specifically, a clear abundance peak can be found at 65–75 m depth (Fig. 6a). While not as clear as in the abundance graph (Fig. 6a), the same tendency can be observed in the density plot (Fig. 6b). In addition, there is a clear density increase of *A. mediterraneus* in the continental shelf below 50 m depth (Fig. 6b). Moreover, between 50 and 90 m depth there are a high number of outliers, with over 100 individuals found (Fig. 6a) and

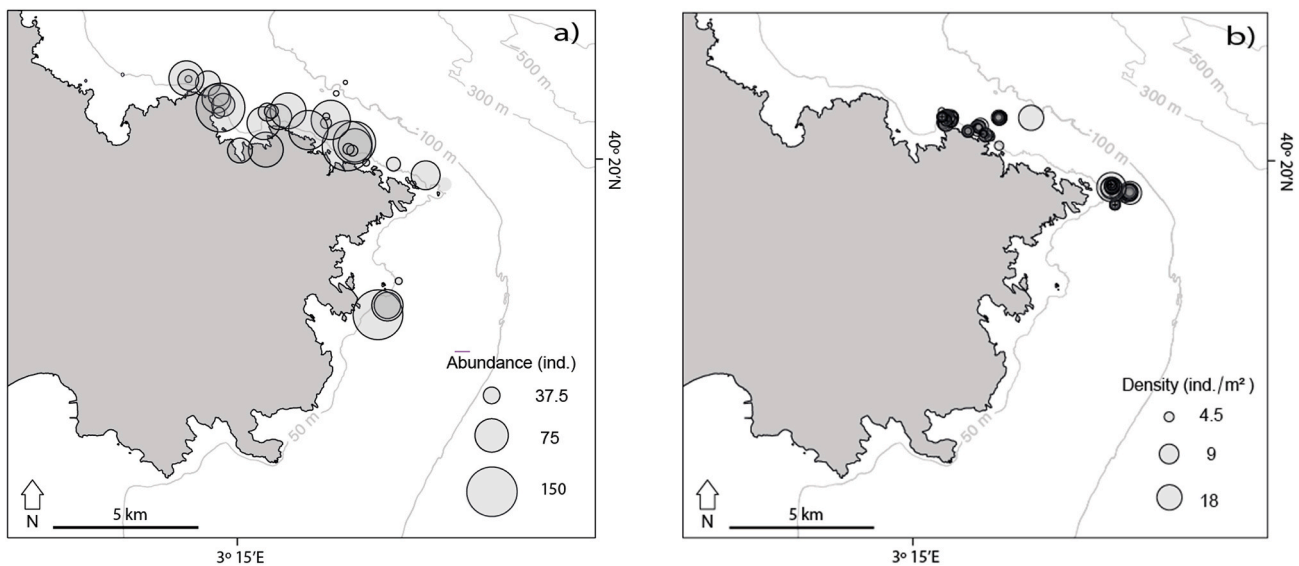


Fig. 5. Geographical distribution of *A. mediterraneus* in the study area, based on by-catch abundance (a) and video transect density (b) data. Projected view UTM Zone 31N (WGS84).

densities of up to 15 ind.  $m^{-2}$  (Fig. 6b). Thus, a remarkable finding is that almost all *A. mediterraneus* individuals were found as by-catch when using trammel nets, versus gillnets and pots (Fig. 6a).

### 3.3. Environmental factors influencing distribution

According to the ANOVA and the following *posthoc* pairwise test, all environmental variables, except DFGs, presented statically significant differences between their evaluated categories (Table 2; See Supplementary material 3). A defined pattern was observed for *A. mediterraneus*, occurring significantly at higher densities towards rocky substrates (0.58 ind.  $m^{-2}$ ), over softer substrates (4.4e-02 ind.  $m^{-2}$ ), and cobbles and pebbles substrate (6.5e-02 ind.  $m^{-2}$ ; Fig. 7a; Table 3. See Supplementary material 4). Regarding the relationship between species density and the presence of ecosystem engineers, there was an evident preference of the basket star for gorgonian forests (90.46%) (Fig. 7b) (Table 3. See Supplementary material 4). However, some individuals were also recorded in habitats dominated by soft corals and barren rocky grounds (9.53% of the total), although with considerably lower densities (2.3e-03 ind.  $m^{-2}$  and 0.028 ind.  $m^{-2}$  respectively, versus 0.31 ind.  $m^{-2}$  for rocky substrates) (Fig. 7a and b; Table 2. See Supplementary material 3). *A. mediterraneus* was also associated with sloping areas, showing a prevalence for this type of habitat (Fig. 8a). Finally, no significant relationship was found between *A. mediterraneus* densities and lost fishing gear (Fig. 8b; Table 2. See Supplementary material 3).

### 3.4. Survey analysis

A total of 26 fishers from nine different guilds of the Catalan coast answered the questionnaire. A fishing experience of 10–15 years is the mean estimated for the collective, based on the guild's estimation. The answers were stated as follows: 69.2% of fishers surveyed perceived an increase in the abundance of basket star individuals on their fishing grounds. Among them, 26.3% stated that between 1 and 20 individuals get caught per fishing gear daily, 31.5% said that they find between 20 and 40 individuals as by-catch in their fishing gear daily, and 42.1% answered that 40 to over 50 basket stars get entangled in their fishing gear each day (Fig. 9a). There is also an important difference between fishers' perceptions depending on the location of their guild along the Catalan coast. Northern and central guilds declared they tend to catch more individuals than those in the south (Fig. 9a and b).

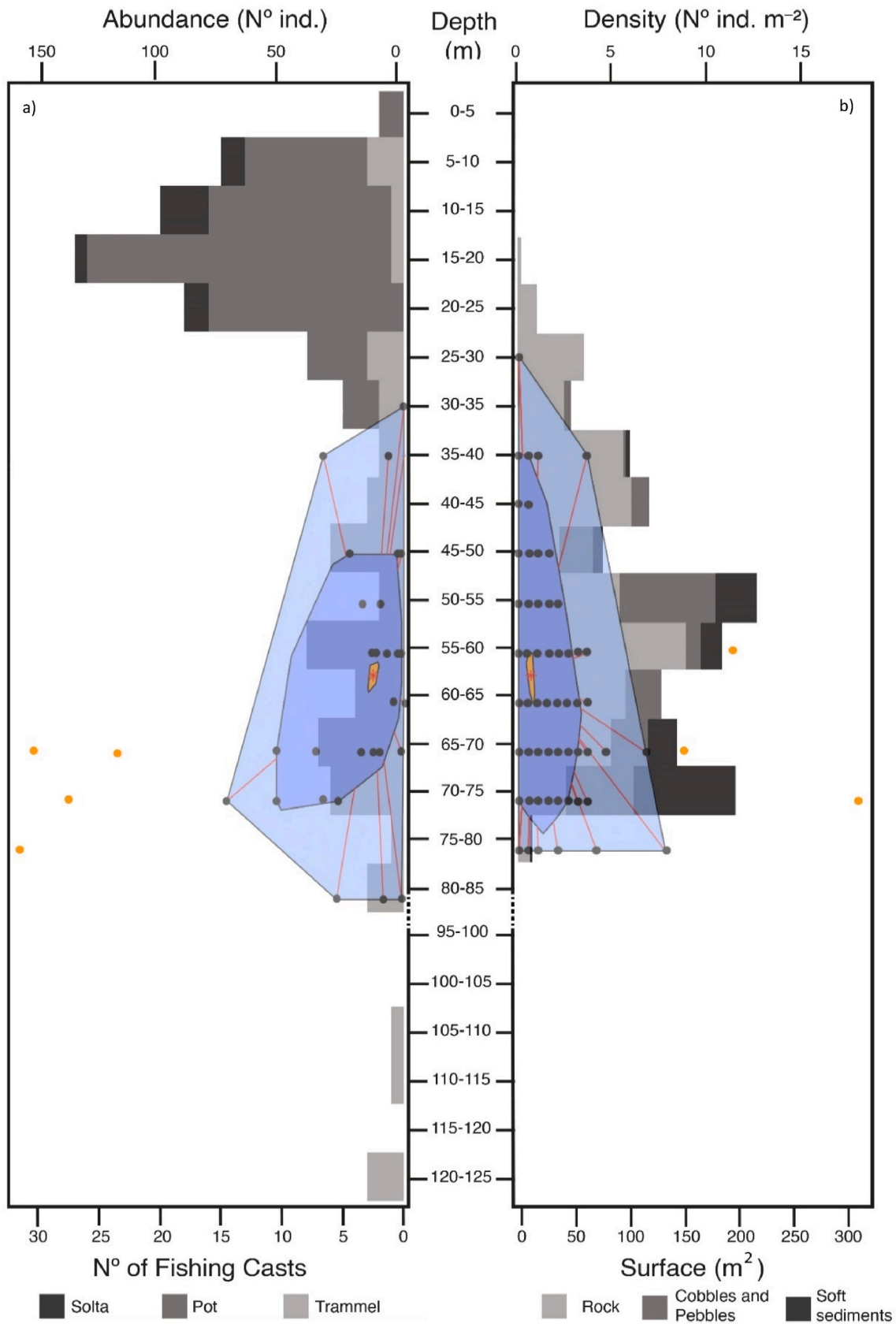
There is unanimity when asked whether they consider basket stars a problem for artisanal fisheries, with all of them agreeing that it constitutes an obstacle to their job performance (Fig. 10). Regarding the guilds involved in the project (Cadaqués and Port de la Selva), all concur on the increase in abundance on their fishing grounds (Fig. 9a), with 75% spending between 1- and 3-h cleaning nets from basket star individuals. About 37.5% stated that between 20 and 40 individuals get caught in their fishing gear each day, and 50% declared that they needed to remove 40 to over 50 basket stars from their fishing gear daily. Regarding the time spent cleaning fishing gear due to the presence of the species, 9.5% spent less than 30 min on this task daily, while 28.5% spent 30 min to 1 h, 47.6% devoted 1–3 h, 4.75% occupied 3–5 h, and 4.7% spent over 5 h cleaning the net from *A. mediterraneus* individuals each day (Fig. 9b). Regarding the economic cost of this by-catch on their fishing gear, they estimate a monetary loss of € 30–100 per week in by-catch cleaning and fixing damaged gears provoked by this species, but all of them coincide in the difficulty in determining a specific quantity.

## 4. Discussion

### 4.1. Species status prior to this study

Prior to this study, limited works on the ecology and distribution of *A. mediterraneus* had been performed. Previous studies mainly focused on sporadic records and brief descriptions of the species (e.g. Risso, 1826; Figuier, 1868; Koehler, 1921) or were mainly taxonomical in nature (Hansson, 1999). Several studies do mention its appearance in specific areas, yet details are sparse, and most of them are an isolated record of its presence (Table 1. See Supplementary material). Nevertheless, some scientific articles had reported local aggregations of the species (Capria, 1893; Cadenat, 1938; Buchanan, 1957; Harmelin et al., 1991; Boavida et al., 2016b), but none of them detailed the potential reasons to explain it nor provided any precise density and/or environmental data regarding said aggregations (Table 1. See Supplementary material).

In this study, a total of 1,800 specimens of *A. mediterraneus* were analyzed, considering both the results of the 19 video transects (890 individuals) and the data from 143 artisanal fishing events (910 individuals). Based on these results, this study provides, for the first time, standardized data regarding the presence of high densities of *A. mediterraneus* in the northwest Mediterranean Sea. Considering the aforementioned scarcity of scientific reports in the Mediterranean Sea,



**Fig. 6.** Bathymetrical distribution of *A. mediterraneus*. **Bagplots** (in blue shades) represent the abundance (a) and density (b) of the species including all depth range intervals. The orange bag with an asterisk represents the median value for water depth, followed by the dark blue polygon (bag), which represents 50% of the total values, and the light blue polygon (fence), representing the values outside said 50%, excluding outliers (orange dots). The **barplot** represents the number of fishing casts and used fishing gear per bathymetric range (a) and the different substrate types along the ROV transects in each water depth range (b).



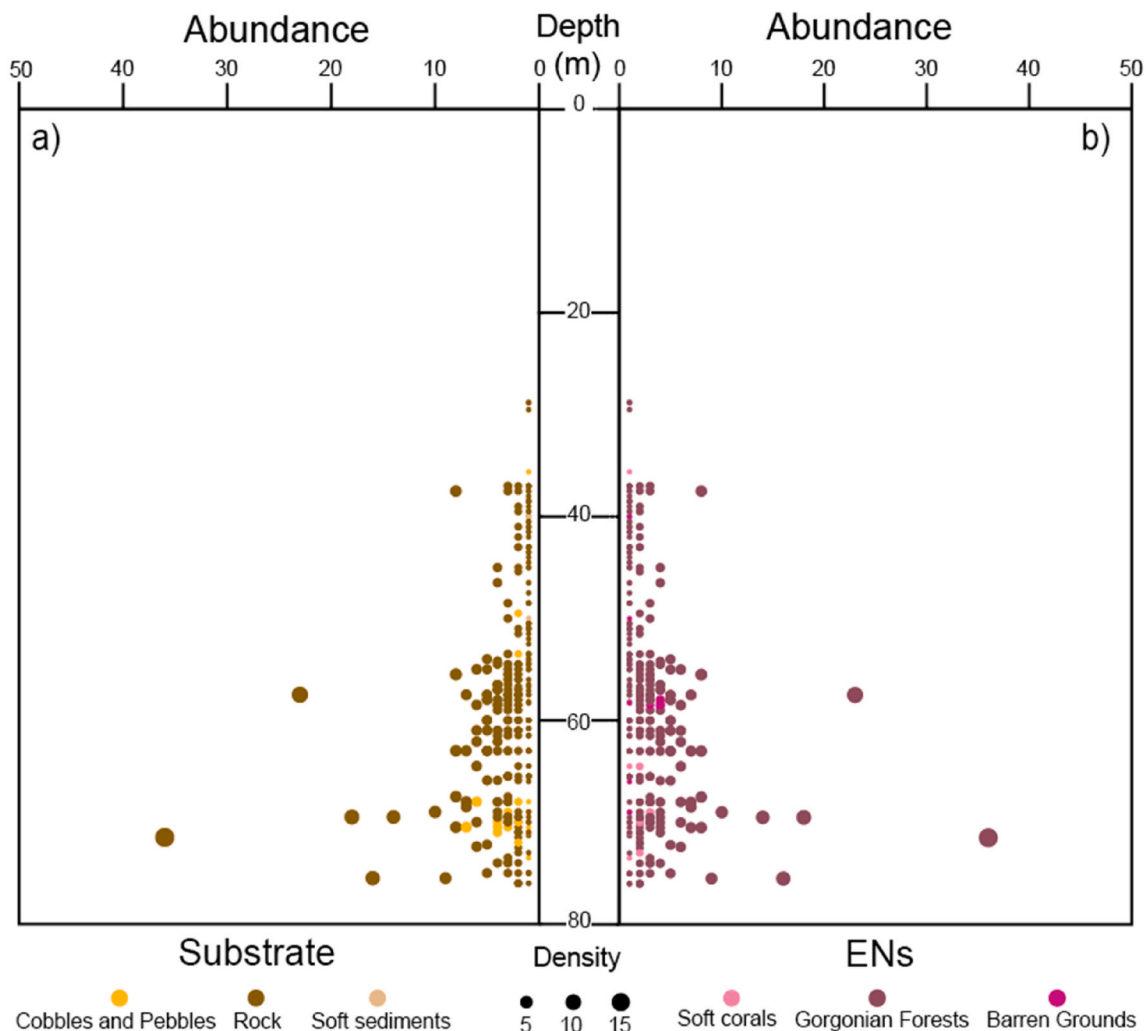


Fig. 7. a, b. Scatterplots showing the relationship between the abundance of *A. mediterraneus* in regard to substrate type (a) and dominating ecosystem engineers (b). Each dot's width represents the density of the study species with depth.

the abundance and density values of *A. mediterraneus* in the study area ( $15.96 \pm 33.49$  mean ind. per trammel net and maximum values of 150 ind. per trammel net and  $0.45 \pm 0.71$  mean ind.m<sup>-2</sup>, respectively) are extremely high, especially on deep rocky sloping substrates with the presence of gorgonian assemblages ( $2.77 \pm 3.18$  mean ind.m<sup>-2</sup>). The following presents a description of the aggregations' characteristics and possible reasons to explain and assess previously unregistered *A. mediterraneus* aggregations.

#### 4.2. Ecological characterization of the basket star aggregations

The high abundances (i.e., over 150 ind. per fishing event) and densities ( $0.45 \pm 0.71$  mean ind.m<sup>-2</sup> and 18 ind.m<sup>-2</sup> maximum values) of *A. mediterraneus* witnessed in the study area, together with the limited amount of observations reported, and little evidence of massive aggregations of this species registered in the Mediterranean Sea (Fig. 1, Table 1. See supplementary material 1), suggest that, as the fishers had suspected, a considerable increase of the species might have occurred in the CdC area. Nevertheless, although the mean number of individuals in the video transects was just  $0.45 \pm 0.71$  ind.m<sup>-2</sup>, basket star density values were not homogeneous along the study area, with dense aggregations of  $1.07 \pm 2.51$  mean ind. m<sup>-2</sup> occurring within a well-defined bathymetric range (i.e., between 55 and 80 m water depth and a peak value of 18 ind.m<sup>-2</sup> at 76 m depth). This could be the result of cryptical behavior displayed by some ophiuroid species (Chesher, 1969), which

might be expressed in different ways, but always with the main aim of avoiding predation and maximizing the organism's ability to conceal itself (McGraw-Hill, 2003). Some species avoid light frequency to elude predation pressure (Diehl, 1988), while others do so because the UV radiation can be damaging to their larval stages (Adams, 2001). Other studies on the photoperiodic activity pattern of ophiuroids showed a well-defined activity, increasing during the no-light and weak light periods (Tsumamal and Marder, 1966; Rosenberg and Lundberg, 2004). In the study area, a strong stratification of the water column occurs during summer due to enhanced irradiance and the warming of shallow waters (Coma et al., 2000, 2009). A pycnocline is formed at around 40–50 m water depth, providing two different water layers during this period. The water below the pycnocline presents higher turbidity and, consequently, lower light penetration (Coma et al., 2000), which provides a more propitious habitat for species with cryptic behaviors. The results of the present study show that *A. mediterraneus* is barely present in waters shallower than 50 m (Fig. 6), where the pycnocline is located. However, a considerable increase in abundance occurs below this depth (Fig. 6), suggesting that this species might present cryptic behavior that could be related to light avoidance.

Relevant ophiuroid aggregations (e.g. *Ophiotrix maculata* (Ljungman, 1872)) have also been observed in areas of the northwestern African slope, where the water column was affected by upwelling processes (Calero et al., 2018). Similar environmental characteristics occur in the CdC coastal areas, where the strong and highly transient northern winds

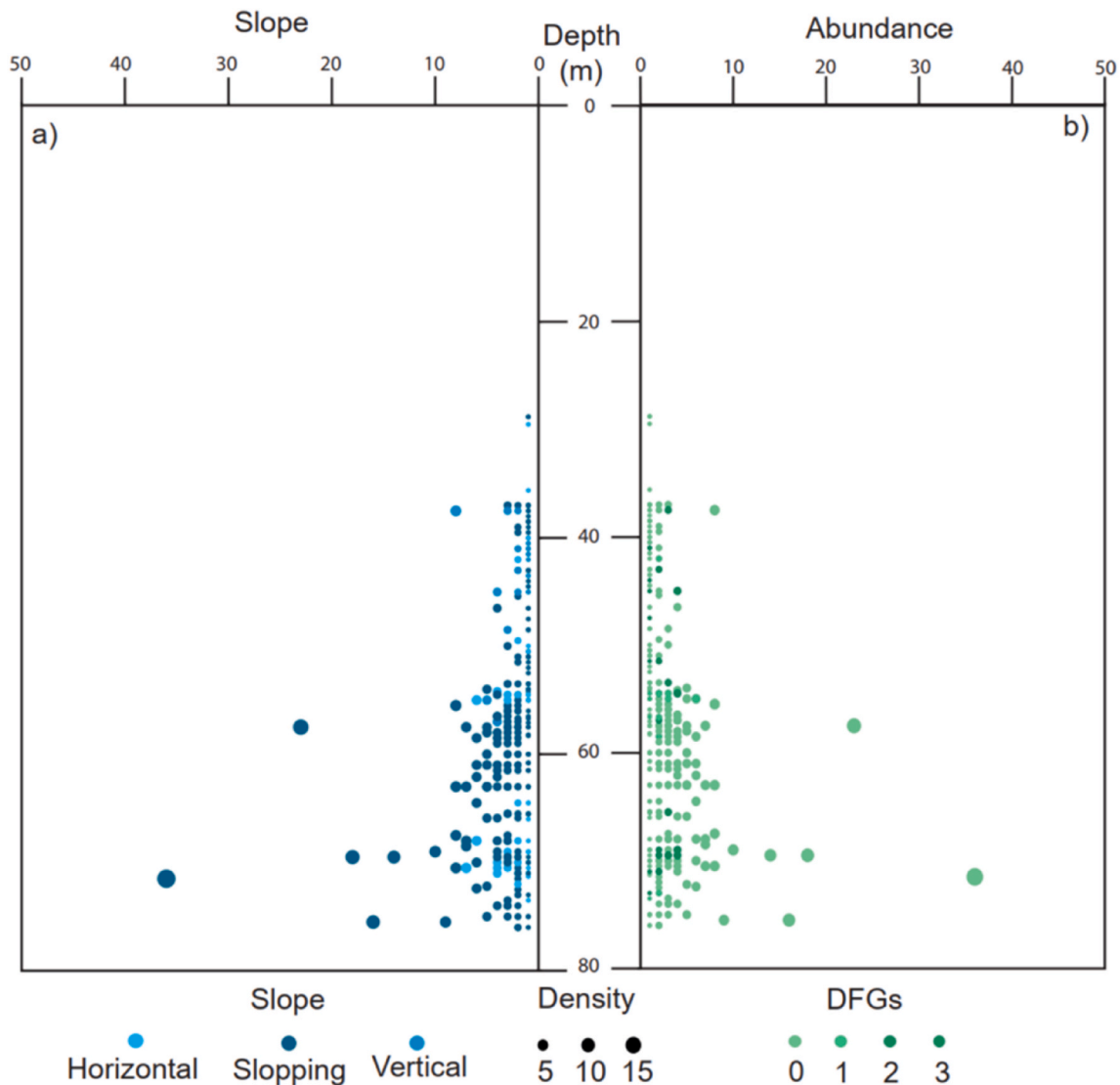
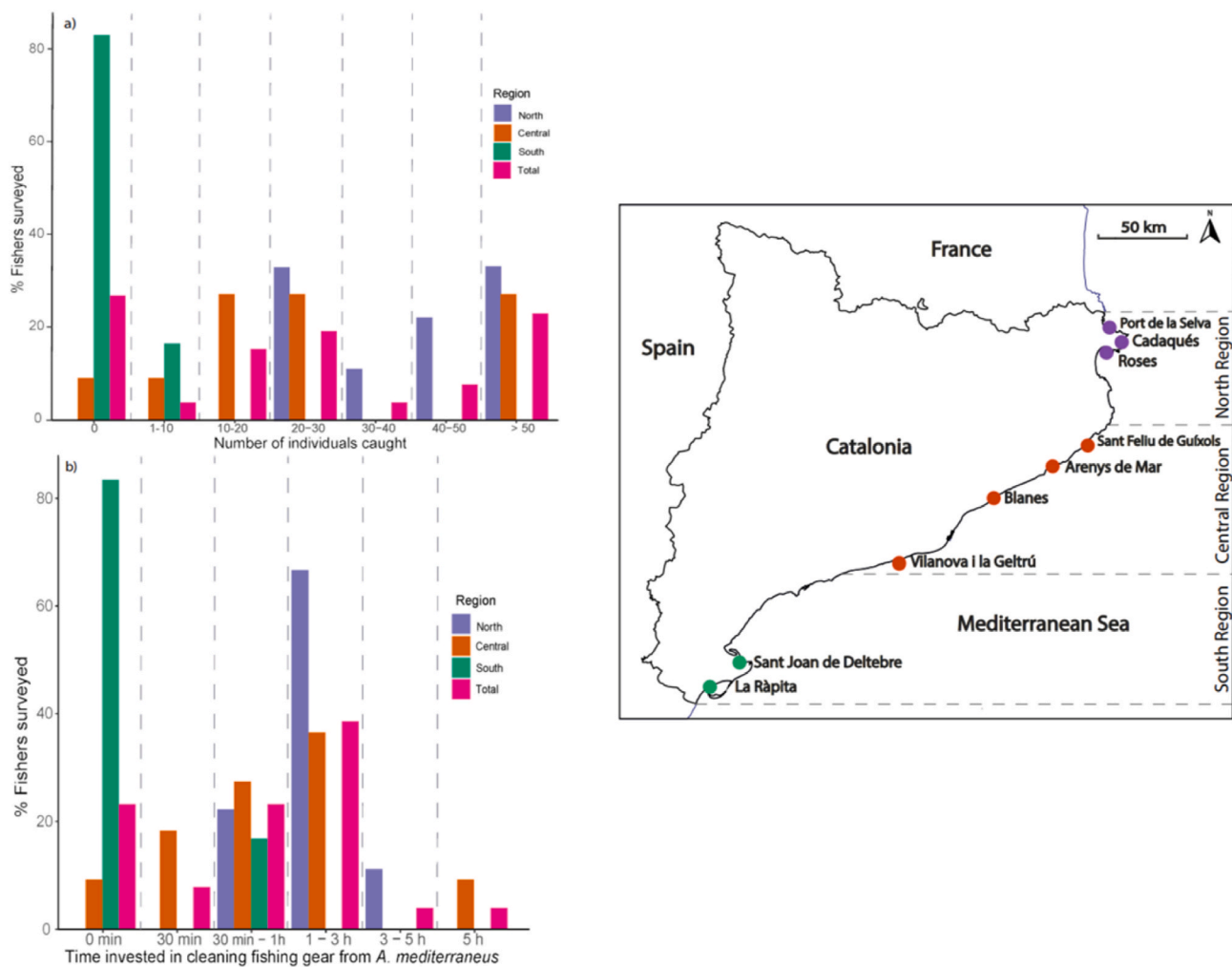


Fig. 8. a, b. Scatterplots showing the relationship between the abundance of *A. mediterraneus*, the seafloor slope (a) and the number of derelict fishing gears (b).

promote the displacement of shallow waters, ultimately fostering upwelling regions that bring nutrients and particulate matter to shallower areas (Millot, 1979; DeGeest et al., 2008; Sardà and Company, 2012). The reduced irradiance and less intense hydrodynamic conditions occurring below 40 m depth and higher food availability (Coma et al., 2000) provide a more suitable environment and an ideal area for the strong prevalence of benthic communities dominated by suspension feeders (Zabala and Ballesteros, 1989; Orejas et al., 2009), including the high abundances of *A. mediterraneus* witnessed here. This is especially true for most of the northern and eastern coasts of the CdC, from Port de la Selva to the Massa d'Or Island and down to Portlligat (Figs. 2 and 5) where coralligenous habitats dwell in areas between 40 and 90 m, forming one of the most ecologically valuable locations of the Natural Park (Rossi et al., 2008; Sardà and Company, 2012). Coincidentally, the highest densities of *A. mediterraneus* mainly occurred in water depths between 50 and 80 m on sloping rocky outcrops, generally dominated by gorgonians (Figs. 7 and 8), which are amongst the most abundant structuring species in the northern part of the CdC continental shelf marine area (Gori et al., 2012; Sardà and Company, 2012). The reason for the strong association between *A. mediterraneus* and gorgonians could reside in the species' feeding mechanism, as basket stars tend to ascend prominences nearby to reach the faster and food-concentrated laminar flow and enhance their food capture by extending their

ramified arms into the dominant current (Boavida et al., 2016; Davis, 1966; Rosenberg et al., 2005). Indeed, this association has been widely reported for several other basket star species across the globe (see Figs. 3d and 11) (Tsurumal and Marder, 1966; Emson et al., 1991; Rosenberg et al., 2005; Boavida et al., 2016). Incidentally, in the CdC marine area gorgonian assemblages are most abundant below the pycnocline, at a similar depth range as where the highest abundances of *A. mediterraneus* were found, including a scarce presence from 90 m depth and below (Gili et al., 2011). Overall, it appears that in the CdC marine area, the summer bathymetrical distribution of the *A. mediterraneus* would seem to be restrained by the depth of the pycnocline formation (40–50 m) at the shallow end. Both traits describe the most suitable environment for the presence of high *A. mediterraneus* densities.

Besides, no link was found between the presence of *A. mediterraneus* and Derelict Fishing Gears (DFGs) in the study area, even though the basket star is frequently captured as by-catch during fishing activities with artisanal trammel nets (Fig. 10). Although other studies had reported an increased abundance of ophiuroids on DFGs (Angiolillo et al., 2015; Oliveira et al., 2015), no significant differences in organism density were observed in regard to DFGs abundance in this study area, despite the prevalence of *A. mediterraneus* in the artisanal fishers' net gears. The high occurrence of the basket star in artisanal trammel nets



**Fig. 9.** Data from the fishers' survey, displaying an estimation of the number of *A. mediterraneus* individuals caught daily in their fishing gear (a), as well as time invested in cleaning their gear due to the presence of *A. mediterraneus* entangled in them (b) according to different regions of the Catalan coast and overall.

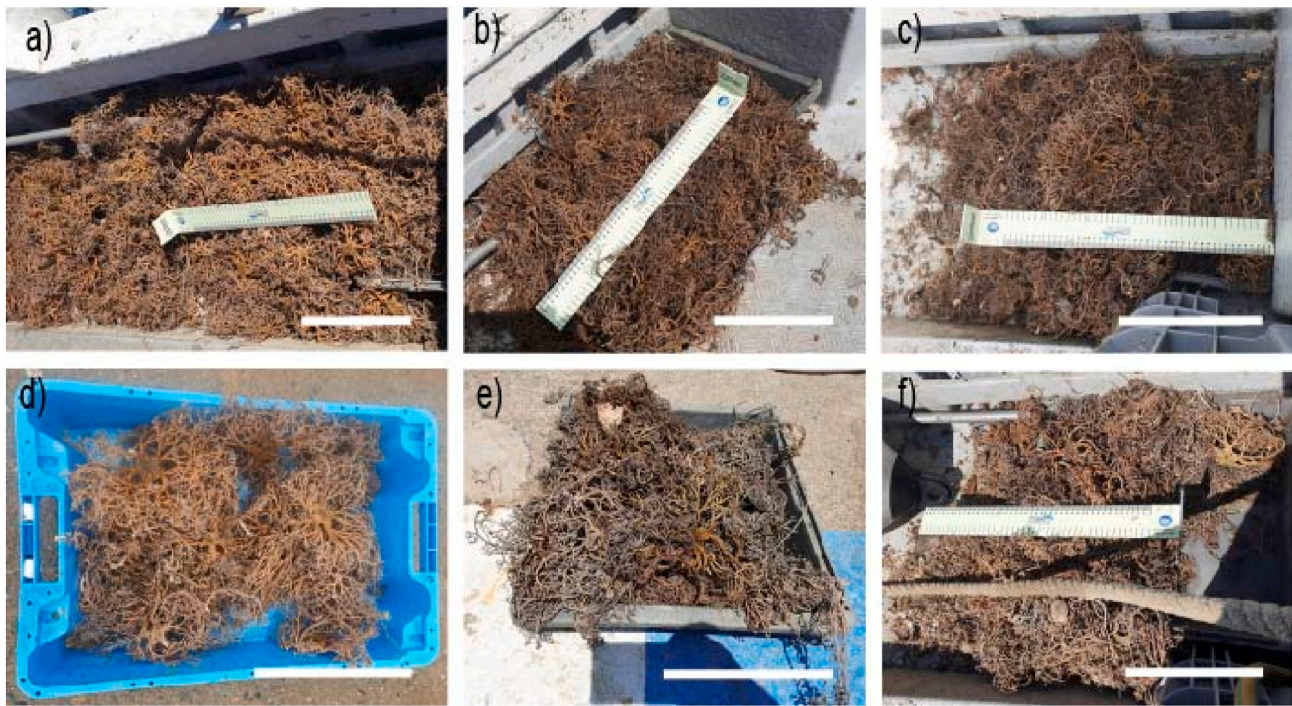
could be caused either by its body structure, having five multibranch arms that might get entangled in the nets, or because the organisms try to climb the fishing gear structure as a means to increase their prey capture, in a similar way to what they tend to do with other benthic structures, including sessile ecosystem engineers (Davis, 1966; O'Hara, 2007). Furthermore, fishers targeting spiny lobsters generally deploy their trammel nets close to rocky outcrops hosting gorgonians (Grinyó et al., 2022), which are the areas of high basket star occurrence. Hence, given the large dimensions of the trammel nets (usually 1.2–1.5 m height x 200 m length), they might provide an extensive substrate with a wider access to the water column than the surrounding habitats, allowing the basket stars to reach areas with faster current velocities and increased food capture probabilities, which might ultimately act as an attraction pool for nearby *A. mediterraneus* individuals. Nevertheless, a potential explanation for the non-significant increase in the species' abundance on DFGs could be that most of them were longlines, which provide extremely limited surfaces to climb on. Additionally, DFGs are not as well set as active fishing nets, commonly bending and folding over and getting profusely entangled, which does not provide the same height and stability as a fishing net when it is being used.

#### 4.3. Population structure of the aggregations in the study area

The size-frequency distribution of the basket star aggregations in CdC was dominated by organisms between 2 and 3 cm (49.04%) followed by 1–2 cm (22.48%) disc diameter, summing up to over 70% of

the analyzed individuals (Fig. 4). Despite the scarce information regarding the demography of the species, the only other study reporting size-frequency data for this species reports individuals with an average of 9.79 cm disc diameter occurring on the Mostaganem coast (Algiers, southwestern Mediterranean Sea) (Benzait and Mezali, 2019). This contrasts with the CdC population, which has a considerably smaller average disc diameter ( $2.67 \pm 0.34$  cm). Several factors, including the absence of any recent proof of established *A. mediterraneus* populations in the CdC marine area (Gili et al., 2011; Domínguez-Carrió et al., 2022) and the fishers' own knowledge regarding the basket star increase in numbers since only a few years ago (Santín et al., 2022), suggest that present-day aggregations in the study area have appeared quite recently. Indeed, this would explain the observed differences in size compared with Algerian populations, as it would point to a recent outburst of relatively young individuals that has given rise to a population structure with smaller disc sizes.

It is important to remark that despite a population skewness towards young individuals, a scarce presence of juveniles ( $\leq 1$  cm) was registered (1.19%) (Fig. 4). This could indicate a bias in the methodology towards medium sizes or could also point towards the possibility that adults, younglings, and larval stages present different ecological requirements. In this sense, there are still huge knowledge gaps regarding ophiuroid embryology and development (Schoener, 1967; McEdward and Miner, 2001; Tominaga et al., 2004). It is known that some Ophiuroidea species have a free-floating larval form referred to as ophiopluteus (Strathmann, 1975; McEdward and Miner, 2001), while others carry out the brooding



**Fig. 10.** Examples of by-catch batches of *A. mediterraneus* individuals accidentally caught in the trammel nets of artisanal fishers from the Port de la Selva and Cadaqués guilds. Each picture corresponds to a single fishing event. The white line corresponds to 25 cm. Author: ICM-CSIC.

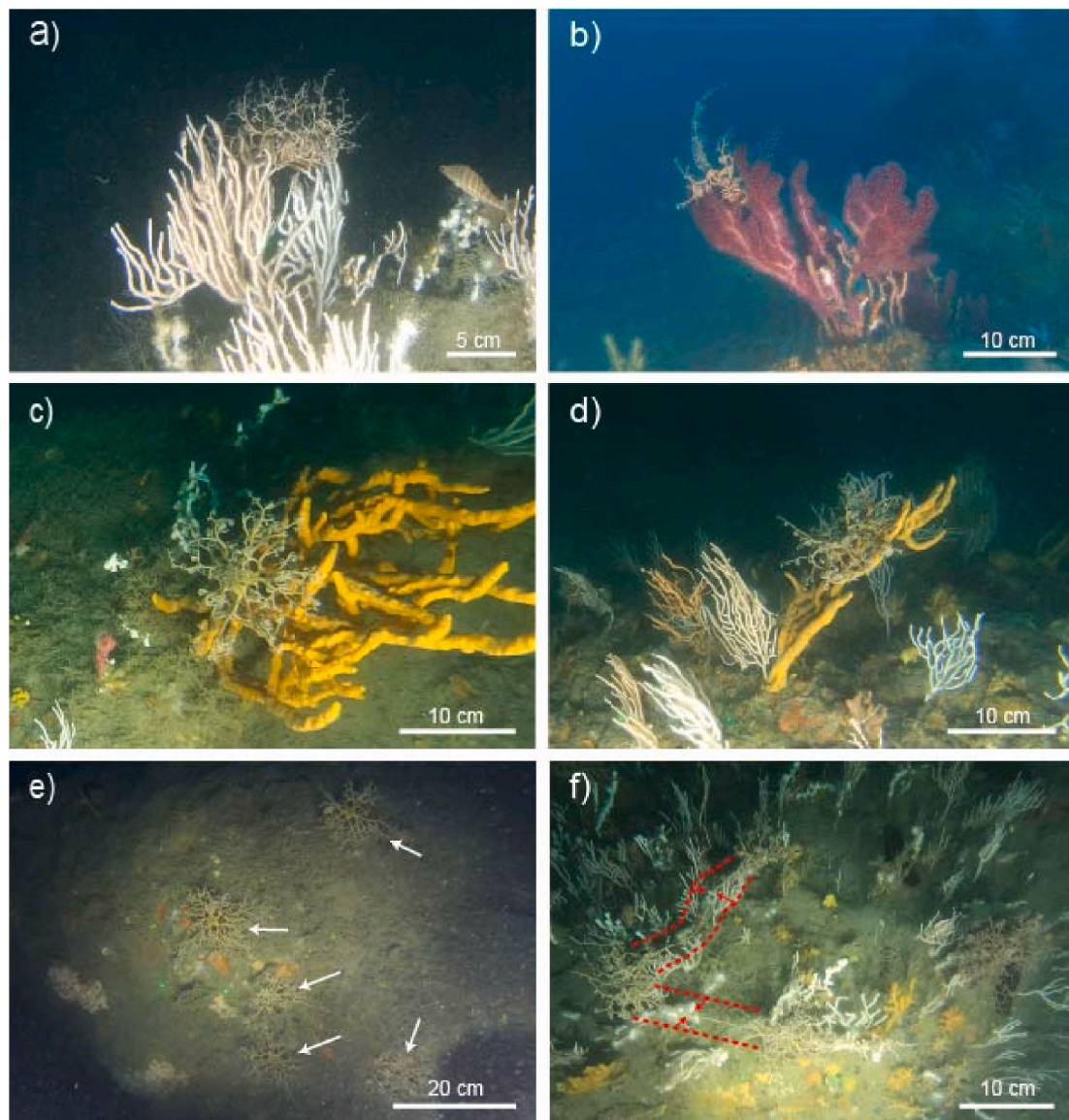
of the larvae in their bursae, giving birth to live juveniles (Schoener, 1967). Yet, no proof of the existence of either of these processes has been found for gorgonacephalids (Patent, 1970a, 1970b; McEdward and Miner, 2001). Growth stages are also an unresolved matter in ophiuroids, as juvenile stages are only known for less than 50 species so far (Stöhr et al., 2012). It is possible that they concentrate in refuge substrates and shift among microhabitats, but their dispersal mechanism is still not fully understood (Hendler and Littman, 1986). Other gorgonacephalid species such as *Gorgonocephalus eucnemis* (Müller and Troschel, 1842) and *Gorgonocephalus chilensis* (Philippi, 1858) have been reported to present young individuals clinging to adults, generally attached to their disk (Clark, 1923; Mortensen, 1923; Fedotov, 1931). This fact could be attributed to a function of passive protection by the adult towards the youngling, or to the young individuals taking advantage of the food captured by the adult until their arms are developed enough to capture food on their own (Fedotov, 1931; Patent, 1970b). The latter phenomenon was also observed in some fishing events during this study, where some small *A. mediterraneus* individuals (less than 1 cm) were found attached to larger ones (Fig. 3c), suggesting that this species may present parental protection. Nonetheless, this was not a common enough observation to be confirmed, and thus further data is needed in this regard.

#### 4.4. Mass occurrence and increasing density growth

Although basket stars' density in the study area has been described to be  $0.45 \pm 0.71$  ind.  $m^{-2}$ , this value is not high enough to consider these habitats as ophiuroid beds, such as the ones reported by Aronson (1992), where densities ranged from hundreds to thousands of individuals per  $m^2$ . Nevertheless, fishers' LEK suggests that the *A. mediterraneus* population in the area has been on the rise for the past years. The data compiled show that current density values are far above those reported for other Mediterranean Sea regions (e.g., Malta:  $2.6 \cdot 10^{-8}$ – $5 \cdot 10^{-7}$  ind.  $m^{-2}$ , Turkey: 2 ind. over 300 km and Libya with 1 individual, first reported in the area; Terribile et al., 2016; Chammem et al., 2019; Leonard et al., 2020; Fitori et al., 2022). While there have not been enough

studies performed on gorgonacephalid ecology to ascertain the exact causes of this potential population outbreak, the answers to this phenomenon might be found in other echinoderm species with registered outbreaks. *Acanthaster planci* (Linnaeus, 1758; Asteroidea), *Amperima rosea* (E. Perrier, 1886; Holothuroidea) and *Amphiura filiformis* (O.F. Müller, 1776; Ophiuroidea), it has been suggested that a plausible cause for the spectacular population outbreaks registered for these species could be linked to an increment both in the quantity and quality of their food source (Duineveld et al., 1987; Josefson et al., 1993). This phenomenon has been suggested to be triggered by water eutrophication (Duineveld et al., 1987; Josefson et al., 1993), increased water temperatures derived from climate change (Billett et al., 2001; Wigham et al., 2003), or rain-derived nutrient enhancement from enriched terrestrial run-off (Birkeland, 1982; Lucas, 1982; Brodie, 1992; Brodie et al., 2005). Under such favorable conditions, both the reproductive output (Billett et al., 2001; Wigham et al., 2003) and the survival of larval stages could be enhanced, potentially leading to multiple and successive recruitment events (Pratchett, 2005). Finally, it is suggested that suspension-feeding species opportunistically boost their biomass in response to higher phytoplankton availability, perhaps acting as a eutrophication-preventing system (Hily, 1991). Concerning the study area, some authors have already considered the CdC marine area a region to be subjected to persistent eutrophic trends (Karydis and Kitsiou, 2011; Tsikoti and Genitsaris, 2021), promoted by high inputs of nutrient-rich waters mainly provided by the Rhône river (Coma et al., 2000; DeGeest et al., 2008) and also by agricultural activities, industrial discharges, and urban effluents (Karydis and Kitsiou, 2011; Tsikoti and Genitsaris, 2021). Annual primary production has remained stable over the past 30 years (Lefevre et al., 1997), and the system balanced over a time scale of decades (Karydis and Kitsiou, 2011). Therefore, considering the area has been eutrophic for a sustained period of time against the recent nature of the basket star bloom, other factors must be considered.

Other cases of echinoderm outbreaks have led to conclude that the overfishing and consequent disappearance of the species' main predators for both for larval and adult stages could have also led to a



**Fig. 11.** Still images extracted from the ROV video transects in the study area. **a-d)** *Astrosparthus mediterraneus* over gorgonian colonies (i.e., *Eunicella cavolini* (**a**) and *Paramuricea clavata* (**b**)) and the sponge *Axinella polypoides* (**c-d**). **e)** Five *A. mediterraneus* individuals on a rocky bottom, marked with white arrows. **f)** Three *A. mediterraneus* individuals over *Eunicella cavolini* colonies with one of their arms extended, reaching for the other individuals (highlighted by dashed red lines). Author: ICM-CSIC.

population increase (Chesher, 1969; Duineveld et al., 1987). For example, the reduction in flatfish stocks in the North Sea caused by the intensification of trawling in the area might have been a decisive factor that may account for the increase in abundance of *Amphiura filiformis* (O. F. Müller, 1776) (Duineveld et al., 1987). Similarly, the depletion of the triton shell *Charonia tritonis* (Linnaeus, 1758) by shell collectors, a predator of the starfish *Acanthaster planci* (Linnaeus, 1758), was suggested to be implicated in the latter's population outbreaks (Chesher, 1969). This might also be analogous to the case in the Mediterranean Sea, where the homologous triton shell *Charonia lampas* (Linnaeus, 1758), which also feeds on echinoderms (Morton, 2012) and has suffered from tremendous population declines in past years, is now being considered a species on the verge of extinction (Cavallaro et al., 2016). Nevertheless, the feeding habits of the *C. lampas* are still under study (Morton, 2012; Cavallaro et al., 2016), and its interaction with or possible predation on *A. mediterraneus* has never been observed. In captivity, young sea bream individuals of the *Diplodus vulgaris* (Forster, 1801), *Diplodus sargus* (Linnaeus, 1758) and *Diplodus annularis*

(Linnaeus, 1758) species, have been registered to graze over the extremities of the basket star (Escoubet et al., 2001). However, such behavior is not documented outside controlled environments. Hence, any possible link or correlation between the population dynamics of these possible predators and that of *A. mediterraneus* is still unknown and thus further research is needed.

While several factors, or a combination of factors, could explain the recorded outburst of *A. mediterraneus* in the area studied, the lack of long-term data and the scarcity of information regarding the ecology and biology of the species studied only allow for a speculative hypothesis on the matter, with the exact causes that have triggered the population outburst remaining unknown.

#### 4.5. Impacts on artisanal fishing

As a result of the surveys conducted, it is clear that basket stars are perceived negatively by the fishers' community as their increase in abundance is associated with an economic loss for artisanal fishers and

constitutes an obstacle to their job performance (Fig. 10). In this sense, fishers state that *A. mediterraneus* by-catch increases fishing gear weight and thus increases dragging on the seafloor; their arms also get entangled the trammel's layers and, overall, they complicate and slow down the extraction maneuver. Additionally, the basket stars (heavily intertwined, coarse and resistant) represent an increase in the time fishers spend cleaning the nets, with an additional economic investment needed to repair the damaged fishing gear.

While there are few studies regarding the economic impact of marine invertebrates on fishers' activity, previous studies focusing on the impact of jellyfish blooms in the North Adriatic concluded that the main elements associated with economic loss were fishing gear deterioration, hours of labor invested, and an associated decrease in catches, amounting to a total estimated economic loss of €8.2 million for otter and mid-water trawling fleets (Palmieri et al., 2014). While they did not provide quantifiable data in terms of economic loss for small-scale fisheries, they did estimate that small-scale fisheries invest over 11,000 h of labor per year in net repair work (Palmieri et al., 2014). In this sense, fishers in the area studied are said to be spending, on average, between one and three extra labor hours daily due to the presence of *A. mediterraneus* in their nets. A possible solution for the fishers affected by this problem would be to modify their fishing habits in order to avoid, or at least reduce, the basket star by-catch incidence on their fishing gear, in a similar way to North Adriatic fishers changing their fishing grounds to avoid jellyfish blooms (Palmieri et al., 2014). Nevertheless, this might not be a solution for artisanal fishers in the study area, as their main targeted species (spiny lobster and scorpion fish) are strongly associated with mid-depth rocky outcrops (Díaz et al., 2001), as is *A. mediterraneus*, which points towards a problem without an immediate solution.

## 5. Conclusions

The ecological traits and habitat preferences of *A. mediterraneus* aggregations in the Cap de Creus marine area have been stipulated for the first time. Basket stars have a habitat preference for sloping rocky substrates with the presence of gorgonians in a water depth ranging between 50 and 80 m. The abundances found are higher than in every other Mediterranean area studied to date and, comparing the central disc size with those of other Mediterranean regions, they can be considered aggregations of young individuals. Despite the fact that *A. mediterraneus*' high abundances were acknowledged only a few years ago and the lack of long time-sensitive data, present study data suggest the beginning or early stages of a massive species outbreak in the area, proving the initial perceptions of a population increase detected by the fishers, and highlighting the importance of considering LEK for ecological studies. However, there is still a massive gap in knowledge regarding the biology of *A. mediterraneus*, and the reasons for this outbreak could not be determined. To properly assess this issue, additional biological studies are needed, as they will be of paramount importance to improve our knowledge on and better understand the origin of the outbreak of *A. mediterraneus* in the Cap de Creus marine area, as well as preventing it from becoming harmful for both the ecosystem and fishers.

With regard to the socioeconomic impact and fishers' perception of this topic, there is unanimity about the existence of a problem associated with this phenomenon. They consider that the increase in basket stars proves a handicap in terms of monetary and time losses, and that the problem should be addressed. The significance of spectacular increases or decreases in echinoderm populations are often challenging to evaluate in terms of long-term averages, since ecological time series, which are seldom available, are needed to determine the scopes of a "natural state". Most possibly, due to environmental and anthropic changes on a local and global scale, phenomena like this will be on the rise, and it is of the utmost importance to investigate them promptly.

## Author contribution

Biel-Cabanelas, Marina: Conceptualization, Investigation, data acquisition, data curation, formal analysis. Writing - original draft; Writing - review & editing. Santín, Andreu: Investigation, conceptualization, methodology, data acquisition, data curation, supervision, Writing - review & editing. Montasell, Mireia: Conceptualization, Investigation, data acquisition, data curation, formal analysis, Writing - original draft. Writing - review & editing. Salazar, Janire: Investigation, conceptualization, methodology, data acquisition, data curation Writing - review & editing. Baena, Patricia: Investigation, data acquisition. Writing Review & Editing. Viladrich, Núria: Investigation, Writing Review & Editing, Montseny, Maria: Investigation, Writing Review & Editing. Corbera, Guillem: Investigation, Formal analysis, data curation, Visualization, Writing Review & Editing, Ambroso, Stefano: Investigation, Writing Review & Editing. Grinyó, Jordi: Funding acquisition, project administration, conceptualization, methodology, data acquisition, supervision, writing-review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

The authors would like to thank the crew of the R/V "Atlantic Explorer", the artisanal fishers from Port de la Selva and Cadaqués and the Cap de Creus Natural Park for their aid. This work was performed under the MitiCap and ResCap projects, which are funded by the *Fundación Biodiversidad* [Biodiversity Foundation] of the *Ministerio para la Transición Ecológica* [Spanish Ministry for Ecological Transition], through the Pleamar Program, co-funded by the European Maritime and Fisheries Fund. In addition, the authors affiliated to the *Institut de Ciències del Mar* [Institute of Marine Sciences] had the institutional support of the "Severo Ochoa Centre of Excellence" accreditation (CEX2019-000928-S). This manuscript is dedicated to memory of Rafael Diego Llinares Bueno, to his family and friends.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.csr.2023.104925>.

## References

- Adams, N.L., 2001. UV radiation evokes negative phototaxis and covering behavior in the sea urchin *Strongylocentrotus droebachiensis*. *Mar. Ecol. Prog. Ser.* 213, 87–95. <https://doi.org/10.3354/meps213087>.
- Allen, J.R., 1998. Suspension feeding in the brittle-star *Ophiothrix fragilis*: efficiency of particle retention and implications for the use of encounter-rate models. *Mar. Biol.* 132, 383–390. <https://doi.org/10.1007/s002270050405>.
- Ambroso, S., Gori, A., Dominguez-Carrió, C., Gili, J.M., Berganzo, E., Teixidó, N., Greenacre, M., Rossi, S., 2013. Spatial distribution patterns of the soft corals *Alcyonium acaule* and *Alcyonium palmatum* in coastal bottoms (Cap de Creus, northwestern Mediterranean Sea). *Mar. Biol.* 160 (12), 3059–3070. <https://doi.org/10.1007/s00227-013-2295-4>.
- Angiolillo, M., Lorenzo, B. di, Farcomeni, A., Bo, M., Bavestrello, G., Santangelo, G., Cau, A., Mastascusa, V., Cau, A., Sacco, F., Canese, S., 2015. Distribution and assessment of marine debris in the deep Tyrrhenian sea (NW Mediterranean Sea, Italy). *Mar. Pollut. Bull.* 92 (1–2), 149–159. <https://doi.org/10.1016/j.marpolbul.2014.12.044>.
- Anscombe, F.J., Glynn, W.J., 1983. Distribution of the kurtosis statistic  $b_2$  for Normal samples. *Biometrika* 70 (1), 227. <https://doi.org/10.2307/2335960>.
- Apple Inc., 2009. Final Cut Pro. Professional Video (7.0.3). <https://www.apple.com/es/final-cut-pro/>.
- Aronson, R.B., 1992. Biology of a scale-independent predator-prey interaction. *Mar. Ecol. Prog. Ser.* 89, 1–13.
- Aswani, S., Lemahieu, A., Sauer, W.H.H., 2018. Global trends of local ecological knowledge and future implications. *PLoS One* 13 (4). <https://doi.org/10.1371/JOURNAL.PONE.0195440>.

- Benzait, H., Mezali, K., 2019. Etude biométrique de l'ophiure profonde *Astropartus mediterraneus* (Risso, 1826) (Ophiuroidea: Echinodermata) des fonds chabutables de la région de Sidi Medjdoub (Mostaganem). *J. Natl. Sci. Nat. Vie.* 41–41.
- Berkes, F., Colding, J., Folke, C., 2000. Rediscovery of traditional ecological knowledge as adaptive management. *Ecol. Appl.* 10 (5), 1251–1262. [https://doi.org/10.1890/1051-0761\(2000\)010\[1251:ROTEKA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[1251:ROTEKA]2.0.CO;2).
- Billett, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.H., Galéron, J., Sibuet, M., Wolff, G.A., 2001. Long-term change in the megabenthos of the Porcupine Abyssal plain (NE Atlantic). *Prog. Oceanogr.* 50 (1–4), 325–348. [https://doi.org/10.1016/S0079-6611\(01\)00060-X](https://doi.org/10.1016/S0079-6611(01)00060-X).
- Birkeland, C., 1982. Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Mar. Biol.* 69 (2), 175–185. <https://doi.org/10.1007/BF00396897>.
- Bivand, R., Keitt, T., Rowlingson, B., 2017. rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 1.2-8. <http://CRAN.Rproject.org/package=rgdal>.
- Bivand, R., Pebesma, E., Gomez-Rubio, V., 2013. *Applied Spatial Data Analysis with R*, second ed. Springer, New York.
- Blaber, S.J.M., May, J.L., Young, J.W., Bulman, C.M., 1987. Population density and predators of *Ophiacantha fidelis* (Koehler, 1930) (Echinodermata: Ophiuroidea) on the continental slope of Tasmania. *Mar. Freshw. Res.* 38 (2), 243–247. <https://doi.org/10.1071/MF9870243>.
- Blanchet-Aurigny, A., 2012. Les populations d'ophiures épigées *Ophiothrix fragilis* et *Ophiocomina nigra* à la pointe de Bretagne: évolution et écologie trophique. PhD Thesis. Université de Bretagne Occidentale. <http://www.theses.fr/2012BRES0041>.
- Boavida, J., Paulo, D., Aurelle, D., Arnaud-Haond, S., Marschal, C., Reed, J., Gonçalves, J.M.S., Serrao, E.A., 2016. A well-kept treasure at depth: Precious red coral rediscovered in Atlantic deep coral gardens (SW Portugal) after 300 Years. *PLoS One* 11 (1). <https://doi.org/10.1371/journal.pone.0147228>.
- BOE., 1998. Ley 4/1998, de 12 de marzo, de Protección de Cap de Creus, 127. Comunidad Autónoma de Cataluña, pp. 17613–17626.
- BOE., 2014. Orden AAA/1299/2014, de 9 de julio, por la que se aprueba la propuesta de inclusión en la lista de lugares de importancia comunitaria de la Red Natura 2000 de los espacios marinos ESZZ16001 Sistema de cañones submarinos occidentales del Golfo de León, ESZZ16002 Canal de Menorca, ESZZ12002 Volcanes de fango del Golfo de Cádiz y ESZZ12001 Banco de Galicia. Ministerio de Agricultura, Alimentación y Medio Ambiente, pp. 58534–58542.
- BOE., 2018. Ley Orgánica 3/2018, de 5 de diciembre, de Protección de Datos Personales y garantía de los derechos digitales. Ministerio de Hacienda y Función Pública.
- Brodie, J.E., 1992. Enhancement of larval and juvenile survival and recruitment in *Acanthaster planci* from the effects of terrestrial runoff: a review. *Mar. Freshw. Res.* 43 (3), 539–553. <https://doi.org/10.1071/MF9920539>.
- Brodie, J., Fabricius, K., De'ath, G., Okaji, K., 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Mar. Pollut. Bull.* 51 (1–4), 266–278. <https://doi.org/10.1016/j.marpolbul.2004.10.035>.
- Buchanan, N.B., 1957. The bottom fauna communities across the continental shelf of Accra, Ghana (Gold Coast). In: *Proc. Zool. Soc. Lond.*, 130. Blackwell Publishing Ltd, Oxford, UK, pp. 1–56. <https://doi.org/10.1111/j.1096-3642.1958.tb00562.x>, 1.
- Cadenat, J., 1938. Liste des échinodermes recueillis pendant la cinquième croisière du navire de recherches Président-Théodore-Tissier (Stellerides, Ophiurides, Echinides). *Rev. Trav. Inst. Pêch. Marit.* 11 (3), 349–375. <https://archimer.ifremer.fr/doc/00000/6907/>.
- Calero, B., Ramos, A., Ramil, F., 2018. An uncommon or just an ecologically demanding species? Finding of aggregations of the brittle-star *Ophiothrix maculata* on the Northwest African slope. *Deep-Sea Res. I Oceanogr. Res. Pap.* 131, 87–92. <https://doi.org/10.1016/j.dsr.2017.11.008>.
- Capria, A., 1893. Appunti anatomici sull' *Astrophyton arborescens*, Müller et Troschel. *Riv. Ital. Sci. Nat.* 13, 115–118.
- Cavallaro, M., Navarra, E., Danzè, A., Danzè, G., Muscolino, D., Giarratana, F., 2016. Mediterranean triton *Charonia lampas lampas* (Gastropoda: Caenogastropoda): report on captive breeding. *Acta Adriat.* 57 (2), 263–272. <https://doi.org/10.32582/aa.57.2.432>.
- Chammem, H., Soussi, J. ben, Pérez-Ruzafa, A., 2019. Checklist with first records for the Echinoderms of northern Tunisia (central Mediterranean Sea). *Sci. Mar.* 83 (3), 195–288. <https://doi.org/10.3989/scimar.04899.19A>.
- Chesher, R.H., 1969. Destruction of pacific corals by the sea star *Acanthaster planci*. *Science* 165, 280–283. <https://doi.org/10.1126/science.165.3890.280>.
- Clark, H.L., 1911. North pacific ophiurans in the collection of the U. S. National Museum. *Bull. U.S. Natl. Mus.* 75, 1–302.
- Clark, H.L., 1923. The Echinoderm Fauna of South Africa. Trustees of the South African Museums.
- Cocito, S., Delbono, I., Barsanti, M., di Nallo, G., Lombardi, C., Peirano, A., 2015. Underwater itineraries at Egadi Islands: marine biodiversity protection through actions for sustainable tourism. *Energ. Amb. Innov.* 61 (4), 69–75. <https://doi.org/10.12910/EAI2015-072>.
- Coma, R., Ribes, M., Gili, J.M., Zabala, M., 2000. Seasonality in coastal benthic ecosystems. *Trends Ecol. Evol.* 15 (11), 448–453. [https://doi.org/10.1016/S0169-5347\(00\)01970-4](https://doi.org/10.1016/S0169-5347(00)01970-4).
- Coma, R., Ribes, M., Serrano, E., Jiménez, E., Salat, J., Pascual, J., 2009. Global warming-enhanced stratification and mass mortality events in the Mediterranean. *Proc. Natl. Acad. Sci. USA* 106 (15), 6176–6181. <https://doi.org/10.1073/PNAS.0805801106>.
- Corbera, G., Iacono, C.L., Gràcia, E., Grinyó, J., Pierdomenico, M., Huvenne, V.A., Aguilar, R., Gili, J.M., 2019. Ecological characterisation of a Mediterranean cold-water coral reef: Cabliers coral Mound Province (Alboran sea, western Mediterranean). *Prog. Oceanogr.* 175, 245–262.
- Courp, T., Monaco, A., 1990. Sediment dispersal and accumulation on the continental margin of the Gulf of Lions: sedimentary budget. *Continent. Shelf Res.* 10 (9–11), 1063–1087. [https://doi.org/10.1016/0278-4343\(90\)90075-W](https://doi.org/10.1016/0278-4343(90)90075-W).
- Davis, W.P., 1966. Observations on the biology of the ophiuroid *Astrophyton muricatum*. *Bull. Mar. Sci.* 16 (3), 435–444.
- DeGeest, A.L., Mullenbach, B.L., Puig, P., Nittrouer, C.A., Drexler, T.M., Durrieu de Madron, X., Orange, D.L., 2008. Sediment accumulation in the western Gulf of Lions, France: the role of Cap de Creus Canyon in linking shelf and slope sediment dispersal systems. *Continent. Shelf Res.* 28 (15), 2031–2047. <https://doi.org/10.1016/j.csr.2008.02.008>.
- Díaz, D., Marí, M., Abelló, P., Demestre, M., 2001. Settlement and juvenile habitat of the European spiny lobster *Palinurus elephas* (Crustacea: Decapoda: Palinuridae) in the western Mediterranean Sea. *Sci. Mar.* 65 (4), 347–356. <https://doi.org/10.3989/scimar.2001.65n4347>.
- Diehl, S., 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos* 53 (2), 207–214. <https://doi.org/10.2307/3566064>.
- Dominguez-Carrió, C., Riera, J.L., Robert, K., Zabala, M., Requena, S., Gori, A., Orejas, C., Lo Iacono, C., Estournel, C., Corbera, G., Ambroso, S., Uriz, M.J., López-González, P., Sardà, R., Gili, J.M., 2022. Diversity, structure and spatial distribution of megabenthic communities in Cap de Creus continental shelf and submarine canyon (NW Mediterranean). *Prog. Oceanogr.* 208, 102877. <https://doi.org/10.1016/j.pcean.2022.102877>.
- Duineveld, G.C.A., Konitzer, A., Heyman, R.P., 1987. *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. *Neth. J. Sea Res.* 21 (4), 317–329. [https://doi.org/10.1016/0077-7579\(87\)90006-8](https://doi.org/10.1016/0077-7579(87)90006-8).
- Ellis, J.R., Rogers, S.I., 2000. The distribution, relative abundance and diversity of echinoderms in the eastern English Channel, Bristol Channel, and Irish Sea. *J. Mar. Biol. Assoc. U. K.* 80 (1), 127–138. <https://doi.org/10.1017/S0025315499001642>.
- Emsen, R.H., Mladenov, P.V., Barrow, K., 1991. The feeding mechanism of the basket star *Gorgonocephalus arcticus*. *Can. J. Zool.* 69 (2), 449–455. <https://doi.org/10.1139/z91-070>.
- Escoubet, S., Woitrain, F., Arnaud, A., Escoubet, P., 2001. A propos d'*Astropartus mediterraneus* et *Centrostephanus longispinus* en captivité. *Bull. Inst. Oceanogr. (Monaco)* 20 (1), 411–414.
- Faria, J.C., Jelihovschi, E.G., Allaman, I.B., 2016. *Fdth: Frequency Distribution Tables, Histograms and Polygons*. UESC, Bahia, Brasil.
- Fedotov, D.M., 1931. Über eigenartigen parasitismus bei stachelhäutern. *Z. Morphol. Und Ökol. Tiere.* 22 (2/3), 401–415. <http://www.jstor.org/stable/43261507>. (Accessed 5 July 2022).
- Figuier, L., 1868. *The Ocean World: Being a Descriptive History of the Sea and its Living Inhabitants*. D. Appleton & Company. <https://www.biodiversitylibrary.org/item/206554>. (Accessed 3 May 2022).
- Fitori, A., Fitori, A. el, Badreddine, A., Aguilar, R., 2022. First record of the basket star *Astropartus mediterraneus* (Risso, 1826) (Echinodermata: Ophiuroidea) in the Libyan waters. *Int. J. Agric. Environ. Sci.* 9 (1), 49–50. <https://doi.org/10.14445/23942568/ijaes-v9i1p109>.
- Garmendia, V., Subida, M.D., Aguilar, A., Fernández, M., 2021. The use of Fishers' knowledge to assess benthic resource abundance across management regimes in Chilean artisanal fisheries. *Mar. Pol.* 127, 104425. <https://doi.org/10.1016/j.marpol.2021.104425>.
- Gili, J.M., Madurell, T., Requena, S., Orejas, C., Gori, A., Purroy, A., Domínguez-Carrió, C., Lo Iacono, C., Isla, E., Lozoya, J.P., Grinyó, J., 2011. Caracterización física y ecológica del área marina del Cap de Creus: Informe final área LIFE+ INDEMARES (LIFE07/NAT/E/000732). Instituto de Ciencias Del Mar/CSIC (Barcelona) Fundación Biodiversidad. <http://hdl.handle.net/10261/171163>.
- Gómez, S., Lloret, J., 2016. La pesca artesanal a Cap de Creus: una mirada al futur. In: *Parc Natural de Cap de Creus. Consell Social Universitat de Girona*, ISBN 978-84-393-9511-9.
- Gondim, A.I., Dias, T.L.P., Christoffersen, M.L., 2015. First record of basket stars *Astrocyclus caecilia* (Lütken, 1856) and *Astrophyton muricatum* (Lamarck, 1816) (Echinodermata, Ophiuroidea, Euryalida) for the state of Rio Grande do Norte, northeastern Brazil. *Check List.* 11 (1) <https://doi.org/10.15560/11.1.1541>, 1541–1541.
- González-Estrada, E., Villaseñor Alva, J.A., Estrada, M.E.G., 2013. Package 'mvShapiroTest'. <https://cran.rproject.org/web/packages/mvShapiroTest/index.html>.
- Gori, A., Viladrich, N., Gili, J., Kotta, M., Cucio, C., Magni, L., Bramanti, L., Rossi, S., 2012. Reproductive cycle and trophic ecology in deep versus shallow populations of the Mediterranean gorgonian *Eumicella singularis* (Cap de Creus, northwestern Mediterranean Sea). *Coral Reefs* 31 (3), 823–837. <https://doi.org/10.1007/s00338-012-0904-1>.
- Grinyó, J., Gori, A., Ambroso, S., Purroy, A., Calatayud, C., Domínguez-Carrió, C., Coppari, M., Lo Iacono, C., López-González, P., Gili, J.M., 2016. Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). *Prog. Oceanogr.* 145, 42–56.
- Grinyó, J., Francescangeli, M., Santín, A., Ercilla, G., Estrada, F., Mecho, A., Fanelli, E., Costa, C., Danovaro, R., Company, J.B., Sobrino, I., Valencia, J., Aguzzi, J., 2022. Megafaunal assemblages in deep-sea ecosystems of the Gulf of Cadiz, northeast Atlantic ocean. *Deep-Sea Res., Part A* 183, 103738. <https://doi.org/10.1016/j.dsr.2022.103738>.

- Hamilton, R., Walter, R., 1999. Indigenous ecological knowledge and its role in fisheries research design: a case study from Roviana Lagoon, Western Province, Solomon Islands. *SPC Tradit. Mar. Resour. Manage. Knowl. Inf. Bull.* 11, 13–25.
- Hansson, H.G., 1999. European Echinodermata Check-List. A Draft for the European Register of Marine Species (Part of "Species 2000") Compiled at TMBL. Tjärnö Marine Biological Laboratory.
- Harmelin, J.G., Zibrowius, H., Arnoux, A., Romana, L., 1991. Evaluation de l'état des peuplements Benthiques du haut-fond St Julien (Région de St Tropez) campagnes Cyana de mars et Juin 1990. <https://archimer.ifremer.fr/doc/00132/24319/>.
- Harris, J.L., MacIsaac, K., Gilkinson, K.D., Kenchington, E.L., 2009. Feeding biology of *Ophiura sarsii* Lütken, 1855 on Banquereau Bank and the effects of fishing. *Mar. Biol.* 156 (9), 1891–1902. <https://doi.org/10.1007/s00227-009-1222-1/TABLES/9>.
- Hendler, G., Littman, B.S., 1986. The ploys of sex: relationships among the mode of reproduction, body size and habitats of coral-reef brittlestars. *Coral Reefs* 5 (1), 31–42. <https://doi.org/10.1007/BF00302169>.
- Hijman, R., 2016. raster: Geographic Data Analysis and Modeling. R package version 2.5-8. <https://CRAN.R-project.org/package=raster>.
- Hily, C., 1991. Is the activity of benthic suspension feeders a factor controlling water quality in the Bay of Brest? *Mar. Ecol. Prog. Ser. Oldendorf* 69 (1), 179–188. <https://doi.org/10.3354/meps069179>.
- Johannes, R.E., 1981. Working with fishermen to improve coastal tropical fisheries and resource management. *Bull. Mar. Sci.* 31 (3), 673–680.
- Johannes, R.E., 1984. Marine conservation in relation to traditional life-styles of tropical artisanal fishermen. *Environmentalist* 4 (7), 30–35. [https://doi.org/10.1016/S0251-1088\(84\)90256-0](https://doi.org/10.1016/S0251-1088(84)90256-0).
- Johannes, R.E., 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol. Evol.* 13 (6), 243–246. [https://doi.org/10.1016/S0169-5347\(98\)01384-6](https://doi.org/10.1016/S0169-5347(98)01384-6).
- Johannes, R.E., Ogburn, N.J., 1999. Collecting grouper seed for aquaculture in the Philippines. *SPC Live Reef Inf. Bull.* 6, 35–48. <https://purl.org/spc/digilib/doc/v26id>.
- Josefson, A.B., Jensen, J.N., Ærtebjerg, G., 1993. The benthos community structure anomaly in the late 1970s and early 1980s—a result of a major food pulse? *J. Exp. Mar. Biol. Ecol.* 172 (1–2), 31–45. [https://doi.org/10.1016/0022-0981\(93\)90087-5](https://doi.org/10.1016/0022-0981(93)90087-5).
- Karydis, M., Kitsiou, D., 2011. Eutrophication and environmental policy in the Mediterranean Sea: a review. *Environ. Monit. Assess.* 184 (8), 4931–4984. <https://doi.org/10.1007/s10661-011-2313-2>.
- Koehler, R., 1921. *Faune de France 1. Paul LeChevalier, Paris, p. 210.*
- Komsta, L., Novomestky, F., 2012. Moments: Moments, Cumulants, Skewness, Kurtosis and related Tests R Package version 0.13. <http://CRAN.R-project.org/package=moments>.
- Lastaras, G., Canals, M., Ballesteros, E., Gili, J.M., Sanchez-Vidal, A., 2016. Cold-water corals and anthropogenic impacts in La Fonera submarine canyon head, Northwestern Mediterranean Sea. *PLoS One* 11 (5), e0155729. <https://doi.org/10.1371/journal.pone.0155729>.
- Lefevre, D., Minas, H.J., Minas, M., Robinson, C., Williams, P.J.L.E.B., Woodward, E.M.S., 1997. Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions. *Deep Sea Res. Part II* 44 (3–4), 801–832. [https://doi.org/10.1016/S0967-0645\(96\)00091-4](https://doi.org/10.1016/S0967-0645(96)00091-4).
- Leonard, C., Evans, J., Knittweis, L., Aguilar, R., Alvarez, H., Borg, J.A., Garcia, S., Schembri, P.J., 2020. Diversity, distribution, and habitat associations of deep-water echinoderms in the Central Mediterranean. *Mar. Biodivers.* 50 (5) <https://doi.org/10.1007/s12526-020-01095-3>.
- Linares, C., Coma, R., Garrabou, J., Díaz, D., Zabala, M., 2008. Size distribution, density and disturbance in two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis*. *J. Appl. Ecol.* 45 (2), 688–699. <https://doi.org/10.1111/j.1365-2664.2007.01419.x>.
- Lloret, J., Cowx, I.G., Cabral, H., Castro, M., Font, T., Gonçalves, J.M.S., Gordo, A., Hoefnagel, E., Matic-Skoko, S., Mikkelsen, E., Morales-Nin, B., Moutopoulos, D.K., Muñoz, M., dos Santos, M.N., Pintassilgo, P., Pita, C., Stergiou, K.I., Únal, V., Veiga, P., Erzini, K., 2018. Small-scale coastal fisheries in European Seas are not what they were: ecological, social and economic changes. *Mar. Pol.* 98, 176–186. <https://doi.org/10.1016/J.MARPOL.2016.11.007>.
- Lo Iacono, C., Orejas, C., Gori, A., Gili, J.M., Requena, S., Puig, P., Ribó, M., 2012. Habitats of the Cap de Creus continental shelf and Cap de Creus canyon, Northwestern Mediterranean. In: *Seafloor Geomorphology as Benthic Habitat*, pp. 457–469. <https://doi.org/10.1016/B978-0-12-385140-6.00032-3>.
- Lucas, J.S., 1982. Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L.). *J. Exp. Mar. Biol. Ecol.* 65 (2), 173–193. [https://doi.org/10.1016/0022-0981\(82\)90043-0](https://doi.org/10.1016/0022-0981(82)90043-0).
- Madurell, T., Covadonga, O., Requena, S., Gori, A., Purroy, A., lo Iacono, C., Sabatés, A., Dominguez-Carrió, C., Gili, J.M., 2012. 3.7 the benthic communities of the Cap de Creus canyon. In: *Mediterranean Submarine Canyons*, p. 123. <https://doi.org/10.13140/RG.2.1.2370.6720>.
- Mallol, S., 2010. La col·lecció zoològica Joan Ortensi de Roses: procés de revisió i recuperació. *Annals de l'Institut d'Estudis Empordanesos* 41, 183–212. <https://doi.org/10.2436/20.8010.01.31>.
- McEdward, L.R., Miner, B.G., 2001. Larval and life-cycle patterns in echinoderms. *Can. J. Zool.* 79 (7), 1125–1170. <https://doi.org/10.1139/cjz-79-7-1125>.
- McGraw-Hill, 2003. *McGraw-Hill Dictionary of Scientific & Technical Terms*, sixth ed. The McGraw-Hill Companies.
- Metaxas, A., Giffin, B., 2004. Dense beds of the ophiroid *Ophiacantha abyssicola* on the continental slope off Nova Scotia, Canada. *Deep-Sea Res., Part A* 51 (10), 1307–1317. <https://doi.org/10.1016/J.DSR.2004.06.001>.
- Migné, A., Davout, D., Gattuso, J.P., 1998. Calcium carbonate production of a dense population of the brittle star *Ophiotrix fragilis* (Echinodermata: Ophiuroidea): role in the carbon cycle of a temperate coastal ecosystem. *Mar. Ecol. Prog. Ser.* 173, 305–308. <https://doi.org/10.3354/meps173305>.
- Millot, C., 1979. Wind induced upwellings in the Gulf of Lions. *Oceanol. Acta* 2 (3), 261–274. <https://archimer.ifremer.fr/doc/00122/23335/>.
- Montseny, M., Linares, C., Viladrich, N., Olariaga, A., Carreras, M., Palomeras, N., Gracias, N., Istenič, K., Garcia, R., Ambroso, S., Santín, A., Grinyó, J., Gili, J.M., Gori, A., 2019. First attempts towards the restoration of gorgonian populations on the Mediterranean continental shelf. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29 (8), 1278–1284. <https://doi.org/10.1002/AQC.3118>.
- Mortensen, T., 1923. Observations on Some Echinoderms from the Trondheim Fjord. *Norske Videnskabs Selskab, Museet*, p. 22.
- Morton, B., 2012. Foregut anatomy and predation by *Charonia lampas* (Gastropoda: Prosobranchia: Neotaenioglossa) attacking *Ophiaster ophioides* (Asteroidea: Ophiasteridae) in the Açores, with a review of triton feeding behaviour. *J. Nat. Hist.* 46, 2621–2637. <https://doi.org/10.1080/00222933.2012.724721>.
- Nédélec, C., Prado, J., 1990. Definition and Classification of Fishing Gear Categories (No. 222). FAO.
- Neis, B., Schneider, D.C., Felt, L., Haedrich, R.L., Fischer, J., Hutchings, J.A., 1999. Fisheries assessment: what can be learned from interviewing resource users? *Can. J. Fish. Aquat. Sci.* 56 (10), 1949–1963. <https://doi.org/10.1139/f99-115>.
- Ocaña, A., Pérez-Ruzafa, A., 2004. Andalusian coast echinoderms. *Acta Granatense* 3, 83–136. <https://doi.org/10.13140/2.1.1494.4960>.
- O'Hara, T.D., 2007. Seamounts: Centers of endemism or species richness for ophiuroids? *Global Ecol. Biogeogr.* 16 (6), 720–732. <https://doi.org/10.1111/j.1466-8238.2007.00329.x>.
- Oliveira, F., Monteiro, P., Bentes, L., Henriques, N.S., Aguilar, R., Gonçalves, J.M.S., 2015. Marine litter in the upper São Vicente submarine canyon (SW Portugal): abundance, distribution, composition and fauna interactions. *Mar. Pollut. Bull.* 97 (1–2), 401–407. <https://doi.org/10.1016/j.marpolbul.2015.05.060>.
- Orejás, C., Gori, A., lo Iacono, C., Puig, P., Gili, J.M., Dale, M.R.T., 2009. Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. *Mar. Ecol. Prog. Ser.* 397, 37–51. <https://doi.org/10.3354/meps08314>.
- Palmieri, M.G., Barausse, A., Luisetti, T., Turner, K., 2014. Jellyfish blooms in the Northern Adriatic Sea: fishermen's perceptions and economic impacts on fisheries. *Fish. Res.* 155, 51–58. <https://doi.org/10.1016/j.fishres.2014.02.021>.
- Patent, D.H., 1970a. The early embryology of the basket star *Gorgonocephalus caryi* (Echinodermata, Ophiuroidea). *Mar. Biol.* 6 (3), 262–267. <https://doi.org/10.1007/BF00347235>.
- Patent, D.H., 1970b. Life history of the basket star, *Gorgonocephalus eucnemis* (Müller & Troschel) (Echinodermata: Ophiuroidea). *Ophelia* 8 (1), 145–159. <https://doi.org/10.1080/00785326.1970.10429556>.
- Paterson, B., 2010. Integrating Fisher knowledge and scientific assessments. *Anim. Conserv.* 13 (6), 536–537. <https://doi.org/10.1111/j.1469-1795.2010.00419.x>.
- Pratchett, M.S., 2005. Dynamics of an outbreak population of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995–1999). *Coral Reefs* 24 (3), 453–462. <https://doi.org/10.1007/s00338-005-0006-4>.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>.
- Risso, A., 1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, 3. F.-G. Levrault. <https://doi.org/10.5962/bhl.title.58984>.
- Rosenberg, R., Dupont, S., Lundälv, T., Sköld, H.N., Norkko, A., Roth, J., Stach, T., Thorndyke, M., 2005. Biology of the basket star *Gorgonocephalus caputmedusae* (L.). *Mar. Biol.* 148 (1), 43–50. <https://doi.org/10.1007/s00227-005-0032-3>.
- Rosenberg, R., Lundberg, L., 2004. Photoperiodic activity pattern in the brittle star *Amphipura filiformis*. *Mar. Biol.* 145 (4), 651–656. <https://doi.org/10.1007/s00227-004-1365-z>.
- Rossi, S., Tsounis, G., Orejas, C., Padrón, T., Gili, J.M., Bramanti, L., Teixidó, N., Gutt, J., 2008. Survey of deep-dwelling red coral (*Corallium rubrum*) populations at Cap de Creus (NW Mediterranean). *Mar. Biol.* 154 (3), 533–545. <https://doi.org/10.1007/S00227-008-0947-6/FIGURES/6>.
- Ruhl, H.A., 2007. Abundance and size distribution dynamics of abyssal epibenthic megafauna in the Northeast Pacific. *Ecol.* 88 (5), 1250–1262. <https://doi.org/10.1890/06-0890>.
- Santín, A., Grinyó, J., Ambroso, S., Uriz, M.J., Gori, A., Dominguez-Carrió, C., Gili, J.M., 2018. Sponge assemblages on the deep Mediterranean continental shelf and slope (Menorca channel, western Mediterranean Sea). *Deep-Sea Res., Part A* 131, 75–86. <https://doi.org/10.1016/J.DSR.2017.11.003>.
- Santín, A., Grinyó, J., Ambroso, S., Baena, P., Biel-Cabanelas, M., Corbera, G., Salazar, J., Montseny, M., Gili, J.-M., 2022. Fishermen and scientists: synergies for the exploration, conservation and sustainability of the marine environment. In: *Martínez de Albéniz, M.V. (Ed.), The Ocean We Want: Inclusive and Transformative Ocean Science*. Institut de Ciències del Mar, CSIC, pp. 77–79. <https://doi.org/10.20350/digitalCSIC/14070>.
- Sardà, F., Company, J.B., 2012. The deep-sea recruitment of *Aristeus antennatus* (Risso, 1816) (Crustacea: Decapoda) in the Mediterranean Sea. *J. Mar. Syst.* 105, 145–151. <https://doi.org/10.1016/j.jmarsys.2012.07.006>.
- Sardà, F., Maynou, F., 1998. Assessing perceptions: do Catalan fishermen catch more shrimp on Fridays? *Fish. Res.* 36 (2–3), 149–157. [https://doi.org/10.1016/S0165-7836\(98\)00102-7](https://doi.org/10.1016/S0165-7836(98)00102-7).
- Savchev, D., Nason, G., Nason, M.G., 2018. Package 'hwwntest'. <https://cran.r-project.org/web/packages/hwwntest/hwwntest.pdf>.



- Schoener, A., 1967. Post-larval development of five deep-sea ophiuroids. *Deep-Sea Res. Oceanogr. Abst. Deep Sea Research and Oceanographic Abstracts* 14 (6), 645–660. [https://doi.org/10.1016/S0011-7471\(67\)80003-2](https://doi.org/10.1016/S0011-7471(67)80003-2).
- Stöhr, S., O'hara, T.D., Thuy, B., 2012. Global diversity of brittle stars (Echinodermata: Ophiuroidea). *PLoS One* 7 (3). <https://doi.org/10.1371/journal.pone.0031940>.
- Strathmann, R.R., 1975. Larval feeding in echinoderms. *Am. Zool.* 15, 717–730. <http://academic.oup.com/icb/article/15/3/717/2077341>.
- Terribile, K., Evans, J., Knittweis, L., Schembri, P.J., 2016. Maximizing MEDITS: using data collected from trawl surveys to characterize the benthic and demersal assemblages of the circalittoral and deeper waters around the Maltese Islands (Central Mediterranean). *Reg. Stud. Mar. Sci.* 3, 163–175. <https://doi.org/10.1016/j.rsma.2015.07.006>.
- Tominaga, H., Nakamura, S., Komatsu, M., 2004. Reproduction and development of the conspicuously dimorphic brittle star *Ophiodaphne formata* (Ophiuroidea). *Biol. Bull.* 206 (1), 25–34. <https://doi.org/10.2307/1543195>.
- Tsikoti, C., Genitsaris, S., 2021. Review of harmful algal blooms in the coastal Mediterranean Sea, with a focus on Greek waters. *Divers* 13 (8), 396. <https://doi.org/10.3390/d13080396>.
- Turnamal, M., Marder, J., 1966. Observations on the basket star *Astroboa nuda* (Lyman) on coral reefs at Elat (Gulf of Aqaba). *Isr. J. Ecol. Evol.* 15 (1), 9–17. <https://doi.org/10.1080/00212210.1966.10688225>.
- Ulses, C., Estournel, C., Durrieu de Madron, X., Palanques, A., 2008. Suspended sediment transport in the Gulf of Lions (NW Mediterranean): impact of extreme storms and floods. *Continental Shelf Res.* 28 (15), 2048–2070. <https://doi.org/10.1016/j.csr.2008.01.015>.
- Uthicke, S., Schaffelke, B., Byrne, M., 2009. A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecol. Monogr.* 79 (1), 3–24. <https://doi.org/10.1890/07-2136.1>.
- Warner, G., 1982. Food and feeding mechanisms: Ophiuroidea. *Echinoderm Nutr.* 161–181. <https://doi.org/10.1201/9781003078920-7/>.
- Warner, G.F., Woodley, J.D., 1975. Suspension-feeding in the brittle-star. *Ophiothrix fragilis*. *J. Mar. Biol. Ass. U.K.* 55 (1), 199–210. <https://doi.org/10.1017/S0025315400015848>.
- Weinberg, S., 1978. The minimal area problem in invertebrate communities of Mediterranean rocky substrata. *Mar. Biol.* 49 (1), 33–40. <https://doi.org/10.1007/BF00390728>.
- Wickham, H., 2016. *Ggplot2: Elegant Graphics for Data Analysis*, second ed. Springer International Publishing.
- Wigham, B.D., Tyler, P.A., Billett, D.S.M., 2003. Reproductive biology of the abyssal holothurian *Amperima rosea*: an opportunistic response to variable flux of surface derived organic matter? *J. Mar. Biol. Assoc. U. K.* 83 (1), 175–188. <https://doi.org/10.1017/S0025315403006957h>.
- Wolf, H., 2019. *ApIpack: Another Plot Package* (No. 190512). <https://cran.r-project.org/package=apIpack>.
- Zabala, M., Ballesteros, E., 1989. Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. *Sci. Mar.* 53 (1), 3–17. <http://hdl.handle.net/2445/32432>.
- Zibrowius, H., 1978. Nouvelles observations de l'ophiure gorgonocéphale *Astrospartus mediterraneus* sur la côte méditerranéenne de France. *Bibliographie annotée et répartition. Trav. Sci.* 4, 157–169.