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Exploring a deep-sea vulnerable marine ecosystem: *Isidella elongata* (Esper, 1788) species assemblages in the Western and Central Mediterranean

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ABSTRACT

The bamboo coral *Isidella elongata* is a key structuring species on deep muddy bottoms, which has suffered severe consequences from bottom-fishing activities, as it often co-occurs with precious fishery resources such as red shrimps. A five-year series of data collected during a scientific trawl survey was used to localize the presence and to characterize the associated megafauna over a wide spatial scale in the Western and Central Mediterranean (Sardinia, South-Central Tyrrhenian, Western Ionian and Southern Adriatic). In addition, the overlap of *I. elongata* hotspots with nursery and spawning areas of three selected species (*Aristaeomorpha foliacea, Aristeus antennatus* and *Galeus melastomus*) was analysed. The sizes of the colonies were analysed in the South-Central Tyrrhenian and the Southern Adriatic. No significant variation over time was observed in the former, while in the latter, the colonies were bigger but showed a decreasing trend over time.

1. Introduction

The bamboo coral *Isidella elongata* (Esper, 1788) is an alcyonacean species (family Isididae) dwelling on soft bottoms at depths ranging between 115 and 1650 m (Bellan-Santini, 1985; Bo et al., 2015b; Chimienti et al., 2019a; Laubier and Emig, 1993; Lauria et al., 2017). This species is considered near-endemic of the Mediterranean Sea (Grasshoff, 1989). It can form extensive aggregations of colonies, called coral gardens or coral forests (Chimienti et al., 2019b; FAO, 2009; Rossi et al., 2017), representing a true *facies* of the bathyal mud biocoenosis (*sensu* Pérès and Picard, 1964), which are mostly found at depths greater than 500 m (Chimienti et al., 2019a; Relini et al., 1986; Rueda et al., 2019).

Isidella elongata, plays an important ecological role like habitat former, as it increases the three-dimensional habitat complexity of the otherwise flat bathyal bottoms with its candelabrum-like shape. Dense patches of bamboo corals constitute a relevant habitat for several fishes and crustaceans to feed and shelter. Their canopy influences the availability of resources and has thus important implications for benthopelagic food webs (Buhl-Mortensen et al., 2010; Mastrototaro et al., 2017; Maynou and Cartes, 2012; Mytilineou et al., 2014).

Some species that take advantage of the bamboo coral canopy are of great commercial interest, such as the red shrimps (*Aristaeomorpha foliacea* and *Aristeus antennatus*) and the Norway lobster (*Nephrops norvegicus*), which do find higher density of preys within *I. elongata* canopy (Maynou and Cartes, 2012). In addition, the arborescent complexity of colonies' branches could further provide a shelter effect against predators (Mastrototaro et al., 2017). These specie associated to the bamboo coral (Cartes et al., 2013; Lauria et al., 2017; Maynou and Cartes, 2012; Spedicato et al., 1998) account for about 5% of all the income of professional fishery in the Mediterranean (STECF, 2019), with increasing landings especially in Italy and Spain, the main producers in Europe (EUMOFA, 2019). A consistent abundance of species of lower economic value, such as *Merluccius merluccius*, *Micromesistius poutassou*, *Phycis blennoides*, *Lepidorhombus boscii*, *Helicolenus dactylopterus* and *Galeus melastomus*, has also been found to be associated with the bamboo coral (Cartes et al., 2013; D'Onghia et al., 2003; Mastrototaro et al., 2017; Mytilineou et al., 2014; Smith et al., 2010).These species are present associated and not to the bamboo coral, but this facies represent in some

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case a breeding and/or feeding area for several species (e.g. *G. melastomus*, *M. merluccius*, *P. blennoides*, *H. dactylopterus*). Because of this, within or adding the two effects, some species show greater biomass and/or size differences within *Isidella* facies (IF) compared to other areas where these facies are absent (Cartes et al., 2013; Mastrototaro et al., 2017; Mytilineou et al., 2014).

Because of their co-occurrence with species of high commercial value, *I. elongata* populations are highly affected by bottom-fishing activities across the basin, as reported in the Catalan Sea, Balearic Sea and Strait of Sicily (Maynou and Cartes, 2012; Lauria et al., 2017; Mastrototaro et al., 2017). Trawlers can cause direct physical damage (D'Onghia, 2019; Maynou and Cartes, 2012) or exert an indirect impact due to alterations of the hydrodynamic and sedimentary conditions, such as sediment resuspension (Piskaln et al., 1998; Purser, 2015; Watling and Norse, 1998), which expose non-retractile polyps colonies to additional damage (Maynou and Cartes, 2012). In addition, its slow growth, recovery rates, recruitment and its long lifespan (Andrews et al., 2002; Krieger and Wing, 2002; Lacharité and Metaxas, 2013; Roark et al., 2006) are peculiar life history traits that further compromise the resilience of *I. elongata* to such perturbations. For this reason, *I. elongata* has been listed in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species as "Critically Endangered'' (Otero et al., 2017). The Marine Strategy Framework Directive has recognized that several fragile deep-sea habitats need protection as Vulnerable Marine Ecosystems (VMEs) (MSFD, 2008), and the IF has been included in the list of VMEs by the General Fisheries Commission for the Mediterranean Sea (GFCM) (FAO, 2009). Moreover, this mud facies has been included in the "Deep Water Engineering benthic invertebrate assemblages'' in the "Dark Habitats Action Plan'' of the Barcelona Convention (UNEP-MAP-RAC/SPA, 2015). Although IF are not included in the Habitat Directive so far (Council Directive 92/43/EEC), the scientific community is highlighting its ecological and biodiversity hot-spot role (Bo et al., 2015a; Chimienti et al., 2019a, 2019b; Rueda et al., 2019) that make this habitat worthy to be part of a special protection system (Otero and Marin, 2019).

Despite the increasing interest in deep-dwelling VMEs (FAO, 2009, 2018), there are still many gaps in our knowledge of these habitats, particularly those structured by *I. elongata* (Gerovasileiou et al., 2019; Lauria et al., 2017; Maynou and Cartes, 2012). Occurrences of *I. elongata* have been registered in both the Western Mediterranean (Chimienti et al., 2019a and references therein; Fabri et al., 2014 and references therein) and the central-eastern part of the basin (Chimienti et al., 2019a and references therein; D'Onghia et al., 2003; Lauria et al., 2017; Mytilineou et al., 2014; Pierdomenico et al., 2016, 2018; 2019; Vafidis et al., 2006). However, information on the Adriatic Sea and other seas of the Central-Eastern Mediterranean is still scarce (Chimienti et al., 2019a), and a proper assessment of the IF distribution over a broad spatial scale is still largely lacking (Gerovasileiou et al., 2019; Mastrototaro et al., 2017; Pierdomenico et al., 2018).

Acquiring substantial knowledge about *I. elongata* is a fundamental step towards developing management plans and introducing sound conservation measures to protect the habitat and all associated species. In the last 30 years, trawling fishery has developed new technologies and even more powerful engines, which have allowed trawlers to expand their activities to greater depths, resulting in a documented increase of fishing pressure (and impact) on deep-sea habitats (FAO, 2009, 2018). Therefore, knowledge about the occurrence and distribution of this vulnerable habitat plays an important management role. In this regard, the Mediterranean International Bottom Trawl Survey (MEDITS) data (Spedicato et al., 2019) are useful to identify the presence of this species on a wide spatial scale. Even though the trawl net is not the best sampler for a quantitative analysis of benthic biocoenosis and it is only limited to the trawlable grounds, it can still be useful for qualitative assessments and spatial analyses on wider study areas than those traditionally sampled for epibenthic communities (Chimienti et al., 2018; Gerovasileiou et al., 2019; Lauria et al., 2017; Petović et al., 2016).

In this study, we analysed the presence of *I. elongata* observed during the experimental trawl survey in four Mediterranean areas: the Sardinian seas, South-Central Tyrrhenian Sea, Southern Adriatic Sea and North-Western Ionian Sea.

The aim was to provide large-scale indications of *I. elongata* distribution, abundance, demography and association with fish assemblages in order to attempt an assessment of the impact on this VME in different geographic areas. In addition, we performed for the first time a population size analysis, where the species displayed its abundance/biomass peak.

2. Materials and methods

2.1. Data collection

Data were collected in the framework of the MEDITS trawl survey for the years 2012–2016 in four Geographical Sub-Areas (GSAs, *sensu* FAO-GFCM): the Sardinian seas (GSA 11), South-Central Tyrrhenian Sea (GSA 10), Southern Adriatic Sea (GSA 18) and North-Western Ionian Sea (GSA 19) (Fig. 1).

The aim of the MEDITS trawl survey is to estimate the abundance, distribution and population structure of species belonging to several taxa in the Mediterranean Sea. It is usually conducted from late spring to midsummer, at a depth between 10 and 800 m (AAVV, 2017). The hauls are located in five bathymetrical strata according to a random-stratified sampling plan. More details on the survey design and sampling methodology are reported in Spedicato et al. (2019).

For the spatial distribution model, we considered the entire pool of hauls performed in the overall investigated depth range and in each GSA (i.e., 1660 hauls, see below for further details). All collected specimens, both demersal and benthic, were analysed in order to link them to the presence of *I. elongata*. For the species assemblage analysis, we considered only those hauls carried out on substrates suitable for the presence of *I. elongata*, and positive to the IF, i.e. those sites showing a probability of presence ≥80% (see the next paragraph). This procedure was adopted to minimize the influence on the analyses of both hauls where the species generally does not occur (e.g. gravel, coarse sand) (Lauria et al., 2017) and those where the presence of the bamboo coral is only occasional.

Morphological parameters of *I. elongata* colonies were also collected for GSAs 10 and 18 (2014–2016). The basal diameter (BD, in millimetres) was measured to infer about the population structure in the study areas. Basal diameter was measured only when morphological features of retrieved colonies allowed to determine with certainty that it was the base of the colony (i.e. presence of at least part of the root-shaped bases of the colony). The sampling with bottom trawlers allowed only in few cases to have entire colonies, in GSA 18. In these cases, also the height (HC, in mm) and width (WC, in mm) were measured, in addition to BD (Fig. 2).

2.2. Data analysis

Given that *I. elongata* can be typically present below 200 m (Chimienti et al., 2019a), the analysis was mostly focused on the basis of a total of 745 sampling hauls covering a depth range between 200 and 800 m (Table 1).

Geographical location of hauls positive to the presence of *I. elongata* were overlapped to seabed substrates' map obtained from EMODnet Geology portal (https://www.emodnet-geology.eu/). Seabed substrate data classifications uses the Folk classification system, composed by 16 classes (Folk, 1980).

We restricted the analysis only to those hauls belonging to the substrate class '*fine muddy and muddy sand*', which is the most representative substrate for *I. elongata* (Lauria et al., 2017). Moreover, we performed a further selection for those hauls used to describe IF, using

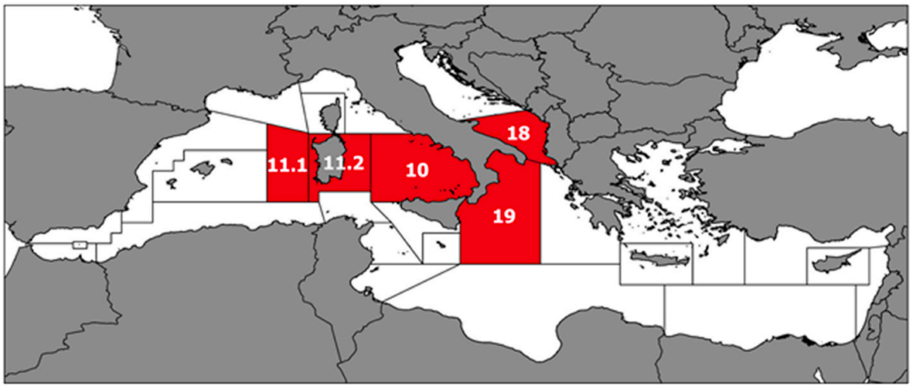

Fig. 1. Map of the studied Geographical Sub-Areas.

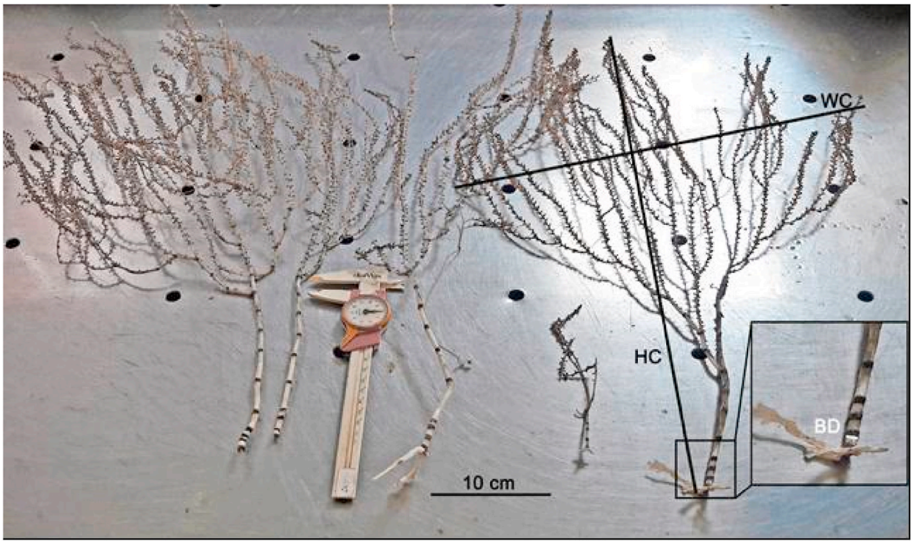

Fig. 2. Size measurements on *Isidella elongata*: height of the colony (HC), width of the colony (WC) and basal diameter (BD).

Table 1
Number of hauls per depth range, year and GSA. GSA: Geographical Sub-Area.

Depth range	GSA 10	GSA 11	GSA 18	GSA 19	Total time series (2012–2016)
10–200 m	29	64	63	27	915
200–800 m	41	38	27	43	745
Total per year	70	102	90	70	1660

only hauls with a probability of presence ≥80% (see below the spatial modelling section).

The number and weight of each species caught were standardized to the swept surface unit (km^2). The density ($N \cdot km^{-2}$) and biomass ($kg \cdot km^{-2}$) indices were then computed according to Souplet (1996). The data on the matrix of biomass per species at each station were compiled using a square-root transformation. The Margalef richness index (d) (Margalef, 1958) was computed for each sampling station in the study areas.

In order to detect potential effects of the presence of *I. elongata* on the species assemblages hauls that showed suitable substrate type (i.e., ‘*fine muddy and muddy sand*’) with a probability of presence ≥80% were pooled into a single category “presence”, while the category “absence” was composed by all remaining hauls on the muddy bottom. The analysis was performed comparing the diversity of the two assemblages at the same GSA (excluding the Sardinian seas due to the low number of hauls positive to the presence of *I. elongata*). The differences between assemblages of each GSA were evaluated using the non-parametric Kruskal–Wallis test (Conover, 1980).

The Bray–Curtis index was used to perform an analysis of similarities (ANOSIM; based on the difference of mean ranks between and within groups) in order to assess the differences in the composition between the assemblages (Clarke, 1993). Moreover, a similarity percentages (SIMPER) analysis was performed to estimate the average contribution of each species to the average overall Bray–Curtis dissimilarity (Clarke, 1993). The ANOSIM analysis was first performed considering all GSAs collectively (excluding the Sardinian seas due to the low number of hauls positive to the presence of *I. elongata*) and also each GSA individually, while the SIMPER analysis was performed only for data from GSA 18, where the differences were significant. All analyses were performed using the R software (R Development Core Team, 2018) and the vegan package (Oksanen et al., 2018).

The spatial distribution of *I. elongata* was assessed using a spatial modelling approach. Specifically, a binomial generalized additive model (GAM) was used to generate a probability map of the presence/absence of the bamboo coral. Presence data were modelled using the binomial family, the logit link function and the following formula:

$$\text{presence} = \alpha + s_1(\text{longitude},\ \text{latitude}) + s_2(\text{depth}) + \varepsilon,\ \text{with}\ \varepsilon \sim N(0.1).$$

A probability map of *I. elongata* presence was generated in the depth range of 200–800 m using a regular grid of point with a resolution of 0.01°. The depth data used to generate the grid were derived from the EMODnet Bathymetry portal. All analyses were performed using the R software (R Development Core Team, 2018) and the mgcv R package.

We also estimated the percentage of overlap of *I. elongata* distribution with Essential Fish Habitats (EFHs) – waters and/or substrates necessary for fish to spawn, breed, feed and grow until the adult stage (Rosenberg et al., 2000) – on particular nursery and spawning grounds of one of the most common selachian species, the blackmouth catshark (*G. melastomus*), and two commercially important shrimps species (*A. foliacea* and *A. antennatus*). Areas corresponding to a presence probability higher than 50%, as derived by the GAM, were considered in the analysis. Data regarding the position and persistence probability of the nursery and spawning grounds of the commercial species were obtained from the Mediterranean Sensitive Habitats project (MEDISEH, 2013). In particular, areas corresponding to a persistence greater than 60% were taken into account. The overlap analyses were performed using the QGIS software (QGIS Development Team, 2017).

Within each area (GSA 10 and 18), the annual median values of colony basal diameter (BD) were used to test the differences in colony sizes in a time frame of three years (2014–2016). The potential differences were tested with Kruskal–Wallis one-way analysis of variance by ranks, and its post-hoc Nemenyi test was used to evaluate the significance of such median differences. To measure the distributions' deviation from symmetry, the skewness (SK) of BD distribution for each GSA was calculated using the R software (R Development Core Team 2018). The skewness can describe three scenarios: (i) distribution dominated by smaller colonies (skewness >0.5), (ii) distribution dominated by larger colonies (negative skewness) and (iii) no size dominance (skewness 0–0.5). The linear relationships of BD *vs* HC and HC *vs* WC were estimated and then they were statistically tested using ANOVA (R Development Core Team, 2018).

2.3. Ethical issue

All the animals used in this study were collected in the framework of the scientific trawl survey MEDITS, authorized in terms of fishing and sampling procedures included the ethical issue (AAVV, 2017), by the Italian Ministry of Agriculture, Food and Forestry Policy MiPAAF (Fishery Department authorization Nos. 15086/2012, 10137/2013, 16101/2014, 10110/2015 and 7973/2016). All animals sampled were already dead when arriving on board. Therefore, the scientific activity in the context of this study is not subject to the European Commission recommendations (Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010) or to Italian National Law (Decree Law No. 26 of 4 March 2014) regarding the protection of animals used for scientific experiments.

Table 2
Depth range and percentage (%) of hauls positive to the presence of *Isidella elongata* for each GSA.

GSA	Depth range (m)	Positive hauls (%)
GSA 10	392–665	30
GSA 11	232–443	2
GSA 18	429–625	23
GSA 19	336–703	11

3. Results

3.1. Distribution

Isidella elongata colony samples were collected at a depth range of 232–703 m in all GSAs, although with different occurrence frequencies in the hauls conducted between 200 and 800 m in depth (Table 2). In the entire period 2012–2016, this bamboo coral was mostly recorded in GSAs 10 and 18, with frequencies of 30 and 23%, respectively, considering all the stations between 200 and 800 m in depth. The species showed lower frequencies in GSAs 11 and 19: 2% and 6%, respectively.

Both the splines of coordinates and depth of the binomial GAM model used to describe the presence probability of *I. elongata* in the study area were significant ($p < 0.05$), with an explained deviance of 56.1%. The residuals were quite normally distributed (Fig. 3). The spline of coordinates (Fig. 4) located the highest probability of bamboo coral presence in the North-Western Sardinian seas, the South-Eastern Tyrrhenian Sea, the North-Western Ionian Sea (along the eastern coast of Sicily) and the southern part of GSA 18 (Otranto Channel). Depths of 500–600 m gave the highest probability of *I. elongata* presence (Fig. 4), as also shown on the model prediction map (Fig. 5).

3.2. Species assemblages

The Margalef index for the two assemblages, with and without *I. elongata* presence, by area is presented in Fig. 6. The assemblages were significantly different ($p = 0.02$; Kruskal–Wallis test) in the Southern Adriatic Sea. No significant differences were observed between the assemblages (with and without *I. elongata*) in the South-Central Tyrrhenian Sea ($p = 0.42$; Kruskal–Wallis test) and North-Western Ionian Sea ($p = 0.36$; Kruskal–Wallis test). This analysis was not performed in the Sardinian seas due to the very low number of hauls positive to the bamboo coral.

The results of the ANOSIM analysis performed in each GSA and in the entire study area are reported in Fig. 7. Significant differences were observed between the two assemblages, with the greatest differences observed in GSA 18 ($p = 0.001$; RANOSIM $= 0.466$). The lack of overlap

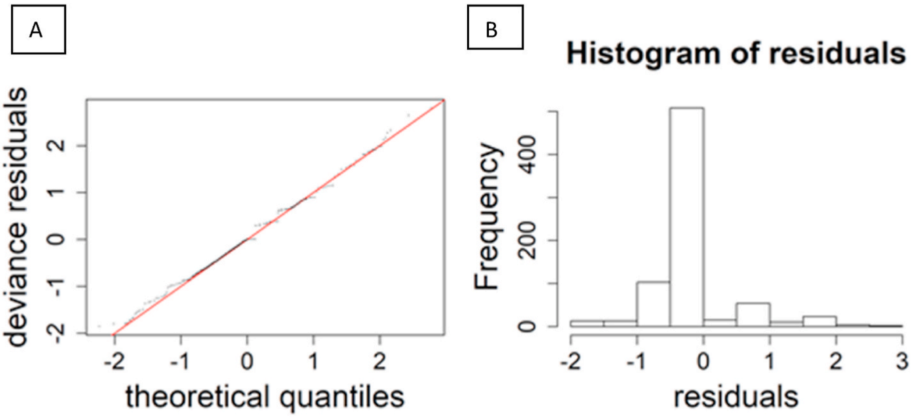

Fig. 3. Diagnostics of model residuals. A: Q-Q plot; B: histogram of residuals.

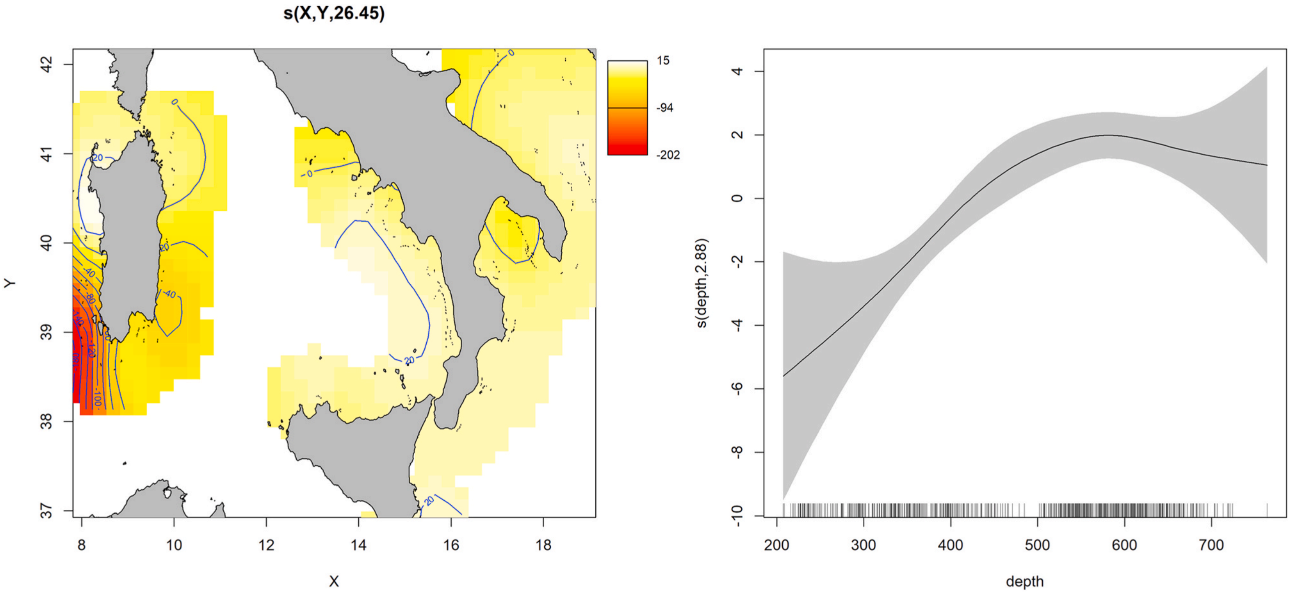

Fig. 4. Partial effect of the model splines.

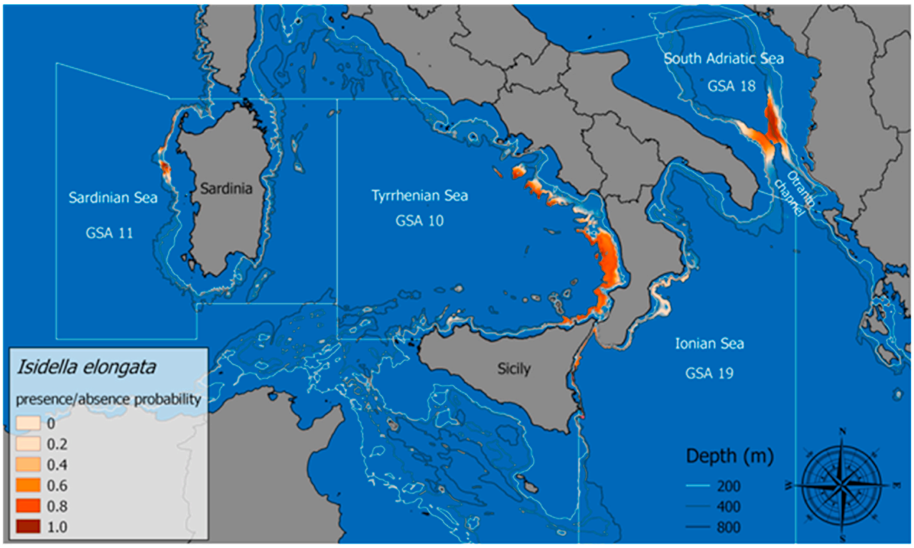

Fig. 5. Prediction map of the probability of bamboo coral presence in the study area.

of box plot areas was considered evidence of the differences between medians (Chambers et al., 1983). The non-significant results observed in GSAs 10 and 19 (GSA 10: $p = 0.719$, RANOSIM = −0.21; GSA 19: $p = 0.744$, RANOSIM = −0.059) were likely due to the low number of hauls positive to *I. elongata* in these areas. Also in this case, the analysis was not performed in Sardinian seas due to the very low number of hauls positive to the bamboo coral.

The SIMPER analysis, conducted only for GSA 18, highlighted the presence of significant differences. The species that contributed to at least 80% of the differences between the assemblages are reported in Table 3. The most important commercial species were the European hake *M. merluccius*, the giant red shrimp *A. foliacea*, the blue and red shrimp *A. antennatus* and the deep-water rose shrimp *Parapenaeus longirostris*. In addition, the spider crab *Anamathia rissoana* and the Mediterranean spiderfish *Bathypterois dubius* were found to be exclusively associated with the IF.

3.3. Overlap between I. elongata facies and Essential Fish Habitats

The percentages of overlap of IF distribution with nursery and spawning areas of the three selected species (*A. foliacea*, *A. antennatus*, *G. melastomus*) are reported in Table 4. The highest percentages were observed with both nursery and spawning areas of *A. foliacea* and only with spawning areas of *A. antennatus* and *G. melastomus*.

3.4. Size distribution

Fig. 8 shows the diameter frequency distributions (DFD) for GSAs 10 and 18, where *I. elongata* showed the highest frequency and abundance. In GSA 10, the colonies ($n = 358$) ranged in BD between 0.50 and 3.83 mm, with the DFD skewed towards small-sized colonies (SK = 0.6175). Results from GSA 18 samples ($n = 468$) showed a BD range of 0.58–6.83 mm, with a wider size distribution and similar proportions of sizes than those in GSA 10. Moreover, the DFD in GSA 18 was more skewed towards larger sizes (SK = −0.0364) compared to that in GSA 10. The

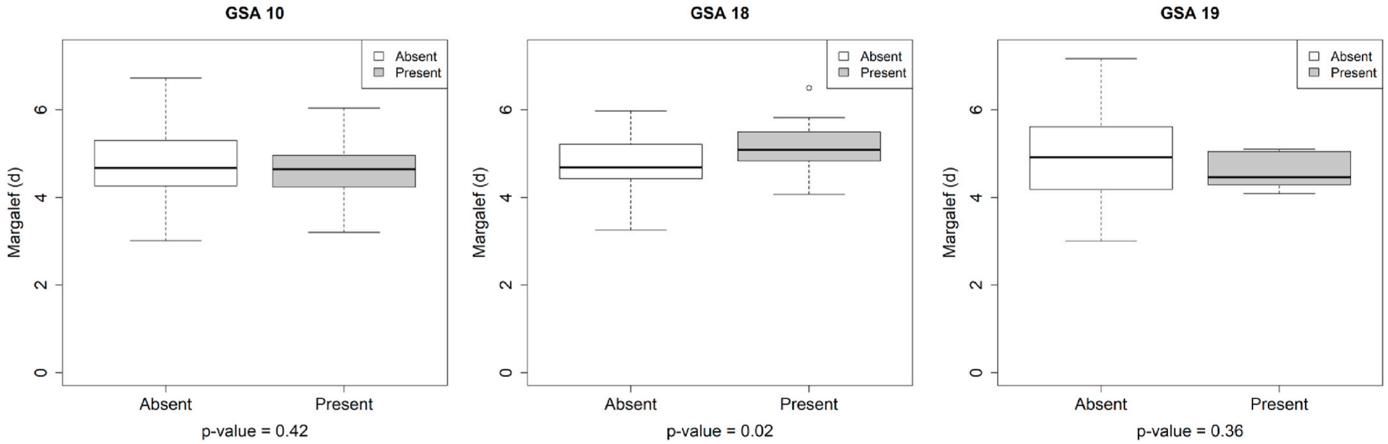

Fig. 6. Box plots of the Margalef index (d) of the assemblages with (Present) and without (Absent) *Isidella elongata* per area. The solid horizontal lines represent median values. Present: haul on the muddy bottom with the probability of bamboo coral presence ≥80%; absent: the hauls on the muddy bottom with the probability of bamboo coral presence <80%. GSA: Geographical Sub-Area.

temporal analysis, comparing the median basal diameter values, showed a progressive decrease over time (from 2014 to 2016) in GSA 18 with significant differences among the years (Kruskal–Wallis test, $H = 0.173$, $p = 6.276e^{-16}$), whereas no similar pattern was observed in GSA 10 without significant differences ($H = 0.0101$, $p = 0.062$) (Fig. 9). The linear relationships of both BD with HC and HC with WC showed a significant positive correlation (Fig. 10).

4. Discussion

Although *I. elongata* can occur at a wide bathymetric range, large populations of this octocoral are currently present mostly below 400 m of depth (Cartes et al., 2009; Ingrassia et al., 2019; Lauria et al., 2017; Mastrototaro et al., 2017; Pierdomenico et al., 2018), probably more due to higher fishing pressures at shallower depths than due to the ecological niche of the species. The bathymetric distribution of the populations reported in this study is in accordance with this general trend, as their upper limits were found at a mean depth of 336 m (302–370 m) in GSA 19, 392 m (364–420 m) in GSA 10 and 429 m (426–432 m) in GSA 18. However, in some areas not impacted by fishing activities, the upper limit of *I. elongata* is shallower (Bo et al., 2015a; Gerovasileiou et al., 2019). In the present study, large aggregations of *I. elongata* were found in shallower waters in the North-Western Sardinian seas, at a mean depth of 232 m (230–234 m), in accordance with findings from the South-Western Sardinian seas (Bo et al., 2015a). Regarding the lower limit of presence of *I. elongata*, the maximum depth reported is 1656 m (Cartes et al., 2013; Maynou and Cartes, 2012). Our results are limited by the sampling protocol of the MEDITS survey, which reaches a maximum depth of 800 m. Thus the sampling area (e.g. trawlable bottom) and the sampler (e.g. trawl net) may bias the understanding of the lower limit of presence (Chimienti et al., 2019a; González-García et al., 2020; Rueda et al., 2016).Therefore, it is difficult to know whether *I. elongata* might be found at greater depths in our study areas as well. However, the greatest depth that we recorded along the Western Ionian (703 m) is comparable to that reported by Mytilineou et al. (2014) for the north-eastern side of this basin (719 m).

The distribution of *I. elongata* is influenced by several factors, some of which have not been fully investigated (Cartes et al., 2013). These factors are linked to the geomorphological (i.e. rugosity, slope) (Cartes et al., 2013; Ingrassia et al., 2019; Lauria et al., 2017), environmental (i.e. substrate, temperature, salinity, strength and direction of currents) (Cartes et al., 2013; Lauria et al., 2017) and trophic characteristics of the habitat (e.g. food availability) (Cartes et al., 2013). In addition, *I. elongata* seems to prefer areas with low seasonal variations in terms of salinity and temperature (Cartes et al., 2013), compact/semi-consolidated mud (Bo et al., 2015a; Pérès and Picard, 1964), moderate currents (Lauria et al., 2017) and high concentrations of near-bottom zooplankton (Cartes et al., 2013). All these features concur to determine the habitat suitability for *I. elongata* in the Mediterranean Basin. Although a modelling of *I. elongata* quantitative data was not carried out due to the limitations of the trawl net as a sampler of the deep benthic communities (González-García et al., 2020), the present results allow us to identify some areas with a high probability of finding *I. elongata*: the Otranto Channel (Southern Adriatic Sea), the east coast of Sicily (Western Ionian Sea), the South-Eastern Tyrrhenian and the north-western coast of Sardinia. These areas exhibit at least some of the above-mentioned characteristics that can drive the presence of the species (Follesa et al., 2009, 2011a; 2011c; Lembo and Spedicato, 2011a; Spedicato and Lembo, 2011a; Tursi et al., 2011). Fishery seems to affect the distribution of the *Isidella* facies (IF) both in terms of presence/density of colonies and in terms of unhealthy conditions (Cartes et al., 2013; Ingrassia et al., 2019; Mastrototaro et al., 2017; Maynou and Cartes, 2012; Pierdomenico et al., 2018). Indeed, the probability of finding IF is higher in areas where trawling activities are difficult due to the presence of submarine canyons (González-García et al., 2020; Pierdomenico et al., 2018, 2019), uneven and/or rocky bottoms (Bo et al., 2015a; González-García et al., 2020) and/or submarine cables (Mastrototaro et al., 2017). Moreover, the presence of several areas characterized by submarine canyons in the Western Mediterranean contributes positively to the presence of *I. elongata*, providing those environmental features needed by the species and offering a natural protection against trawling especially at depths greater than 800 m (Cartes et al., 2013; González-García et al., 2020).

As our surveys were conducted on trawlable bottoms, it was possible to associate the probability of finding IF with both ecosystem characteristics and localized trawling effects. The existence of an area with a high probability of *I. elongata* presence in the Southern Adriatic Sea could be explained by the environmental characteristics of the basin. In fact, the Southern Adriatic vortex produces a water upwelling from its centre; furthermore, the water masses in the Southern Adriatic pit contribute to the entire Mediterranean deep water mass circulation (one of three main areas known thus far in the Mediterranean) with a flow of nutrient-rich deep waters (Vilibić and Orlić, 2002). However, the trawlers' fishing behaviour can also explain the persistence of *I. elongata* in the Southern Adriatic Basin, since the activity of trawler fleets in this GSA is more concentrated on the continental shelf and on the upper part of the slope having as target species the European hake, red mullet, spottail mantis shrimp, deep-water rose shrimp and Norway lobster (Lembo and Spedicato, 2011b), thus probably preserving the deeper IFs. On the contrary, the trawl fishing activity in the Western Ionian is

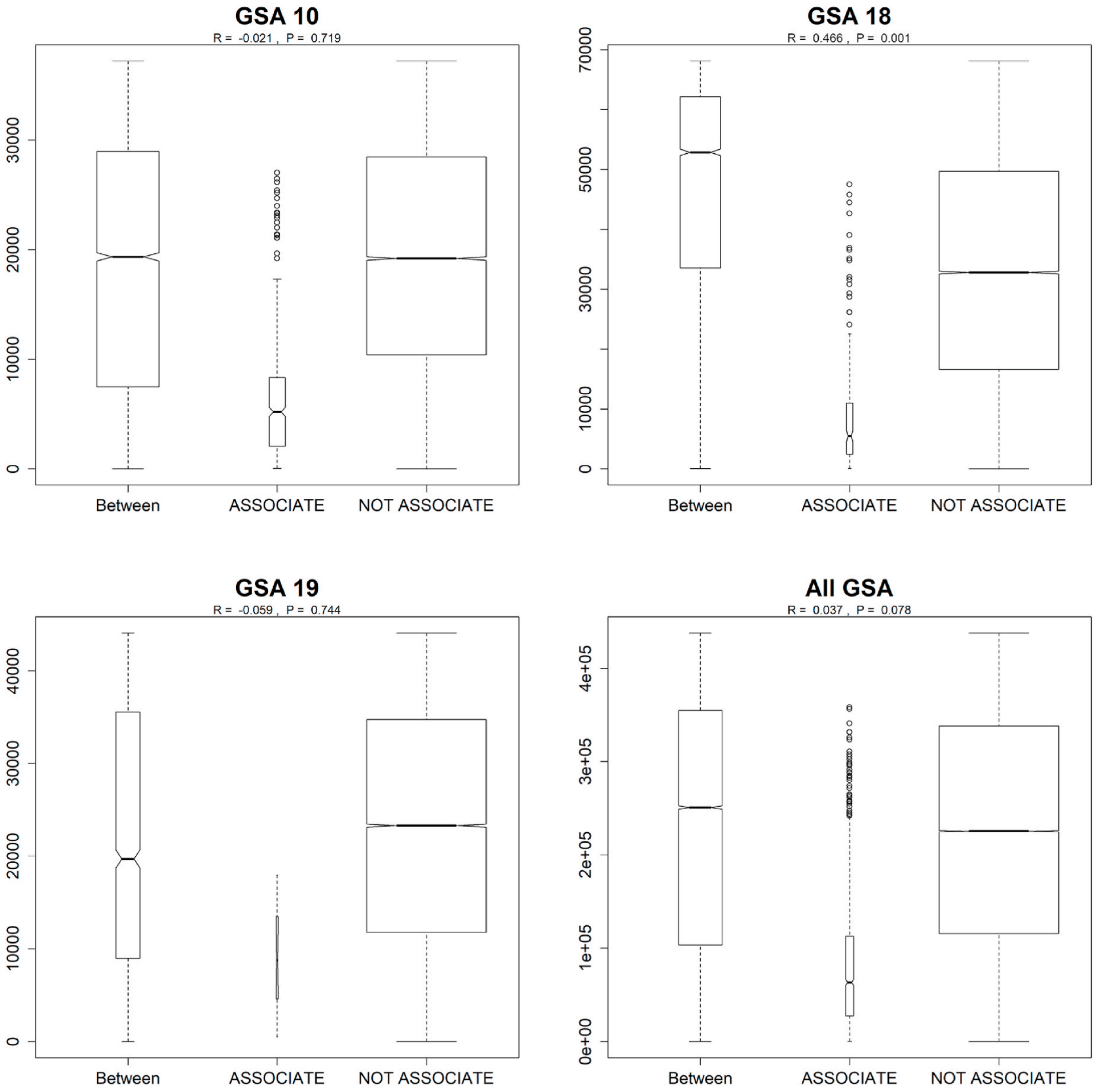

Fig. 7. Analysis of similarities (ANOSIM) plot showing the dissimilarity between and within the two assemblages (with or without *Isidella elongata*) in GSAs 10, 18 and 19 and in the pooled GSAs. Median: bold horizontal bar in the boxes; 25th percentile: bottom of boxes; 75th percentile: top of boxes. Each box width is directly proportional to the sample size. GSA: Geographical Sub-Area.

concentrated on the slope (down to a depth of 200 m), with the blue and red shrimp (*A. antennatus*) and the giant red shrimp (*A. foliacea*) as the main target species (Carlucci et al., 2006; D'Onghia et al., 2005; Maiorano et al., 2010; Russo et al., 2017). Thus, the probability of IF presence in this area currently seems to be lower than in GSAs 10 and 18 due to the fishing impact. Moreover, this species seems to have almost disappeared from the north-western part of GSA 19 (Chimienti et al., 2019a, 2019b; D'Onghia et al., 2003), as well as from the Sardinian seas, where trawlers also operate on deep bottoms (Follesa et al., 2011b). It is also worth underlining that the presence of submarine canyons and/or rocky areas may have protected some pristine bottom enclaves from fishery, where some coral gardens occur, consisting not only of IF but also of black coral (e.g. *Leiopathes glaberrima*), gorgonian (e.g. *Callogorgia verticillata*) and sea pen (e.g. *Funiculina quadrangularis*) aggregations (Bo et al., 2015a; Moccia et al., 2019; Mytilineou et al., 2014). The high probability of IF presence in the Southern and Central Tyrrhenian could also be explained by the fact that even in this area there are favourable environmental conditions, with complex influencing the circulation of water masses on the seabed (Budillon et al., 2009), and with the dense Tyrrhenian deep water playing a crucial role in the deep circulation in the western basin (Millot et al., 2006). Furthermore, trawlers target the red shrimps only during certain months of the year (Spedicato and Lembo, 2011b), thus having a time-limited impact on the IF.

Anthropogenic activities have both direct and indirect impacts on IF health and survival. Remotely operated vehicle (ROV) inspections on soft bottoms with IF have clearly demonstrated that trawling activity adversely affects the IF both qualitatively and quantitatively (Cartes et al., 2013; Mastrototaro et al., 2017). Pierdomenico et al. (2018) found differences in *I. elongata* colonies between untrawled and trawled bottoms of the South-Eastern Tyrrhenian Sea, with a higher percentage of dead and small colonies in the latter.

Data on life history traits of habitat-structuring species, such as age and growth, are essential for understanding their sensitivity and potential recovery from disturbance (Andrews et al., 2002). Unfortunately, the limitations imposed by the trawl survey as well as the mechanical damages allow us to collect few specific data, such as maximum height, branching patterns (width colony) and/or colony vitality; however, it

Table 3

Results of the similarity percentage (SIMPER) of the *Isidella elongata* assemblages in GSA 18. AvSim: average similarity; Sim/SD: ratio of the similarity average to the standard deviation; Contrib%: percentage contribution; Cum%: cumulative percentages; Bio with *Isidella*: average biomass (kg·km^{-2}) for the hauls positive to the presence of *I. elongata*; Bio no *Isidella*: the average biomass (kg·km^{-2}) for the hauls negative to the presence of *I. elongata*.

Species	AvSim	Sim/SD	Contrib%	Cum%	Bio with *Isidella*	Bio no-*Isidella*
Hoplostethus mediterraneus mediterraneus Cuvier, 1829	0.107	1.304	12.189	12.189	27.686	18.838
Galeus melastomus Rafinesque,1810	0.079	1.568	8.991	21.180	43.786	44.859
Merluccius merluccius (Linnaeus, 1758)	0.063	1.034	7.162	28.342	24.541	44.078
Phycis blennoides (Brünnich, 1768)	0.061	1.718	6.933	35.275	13.806	10.338
Helicolenus dactylopterus (Delaroche, 1809)	0.052	1.081	5.989	41.264	14.241	7.042
Illex coindetii (Vérany, 1839)	0.050	0.773	5.745	47.009	3.323	19.694
Etmopterus spinax (Linnaeus, 1758)	0.031	1.293	3.527	50.536	7.710	6.093
Aristaeomorpha foliacea (Risso, 1827)	0.028	1.286	3.240	53.776	14.769	10.674
Pagellus bogaraveo (Brünnich, 1768)	0.026	0.714	2.952	56.728	8.632	8.946
Coelorinchus caelorhincus (Risso, 1810)	0.023	1.298	2.658	59.387	11.212	9.717
Dalatias licha (Bonnaterre, 1788)	0.018	0.334	2.093	61.479	23.993	20.346
Scyliorhinus canicula (Linnaeus, 1758)	0.017	0.417	1.943	63.422	35.322	39.697
Aristeus antennatus (Risso, 1816)	0.017	0.368	1.937	65.359	13.224	6.472
Lophius budegassa Spinola, 1807	0.016	0.564	1.859	67.218	16.964	14.245
Nezumia sclerorhynchus (Valenciennes, 1838)	0.016	1.397	1.827	69.045	6.983	5.715
Lophius piscatorius Linnaeus, 1758	0.015	0.245	1.755	70.800	66.271	37.472
Parapenaeus longirostris (Lucas, 1846)	0.012	0.590	1.399	72.199	4.246	10.041
Todarodes sagittatus (Lamarck, 1798)	0.012	0.790	1.385	73.584	13.478	9.691
Eledone cirrhosa (Lamarck, 1798)	0.012	0.508	1.384	74.968	3.722	10.024
Micromesistius poutassou (Risso, 1826)	0.012	0.418	1.383	76.352	6.676	21.446
Todaropsis eblanae (Ball, 1841)	0.012	0.564	1.349	77.701	7.288	12.214
Chimaera monstrosa Linnaeus, 1758	0.012	0.758	1.330	79.031	10.075	4.933
Paromola cuvieri (Risso, 1816)	0.011	0.724	1.294	80.325	7.269	6.840

Table 4

Overlap percentage of *Isidella elongata* hotspots (occurrence probability >50%) with nursery and spawning hotspots of commercial species (persistence >60%).

	GSA	Species hotspot (km^2)	*Isidella elongata* 50% probability (km^2)	Overlap area (km^2)	Overlap percentage
Spawners *Aristeus antennatus*	GSA 10	305.52	3455.82	88.73	29.04%
	GSA 11	280.60	317.94	0.00	0.00%
	GSA 18	601.70	1482.34	133.56	22.20%
	GSA 19	744.47	468.41	0.00	0.00%
	All GSAs	1932.30	5724.51	222.29	11.50%
Recruits *Aristaeomorpha foliacea*	GSA 10	631.15	3455.82	272.08	43.11%
	GSA 11	not available	317.94	not available	not available
	GSA 18	149.76	1482.34	60.96	40.71%
	GSA 19	3.85	468.41	0.00	0.00%
	All GSAs	784.77	5724.51	278.17	35.45%
Spawners *Aristaeomorpha foliacea*	GSA 10	885.35	3455.82	721.60	81.50%
	GSA 11	308.33	317.94	0.00	0.00%
	GSA 18	256.26	1482.34	80.96	31.59%
	GSA 19	276.99	468.41	0.00	0.00%
	All GSAs	1726.93	5724.51	727.70	42.14%
Spawners *Galeus melastomus*	GSA 10	1131.20	3455.82	469.64	41.52%
	GSA 11	not available	317.94	not available	not available
	GSA 18	176.98	1482.34	118.10	66.73%
	GSA 19	273.12	468.41	0.00	0.00%
	All GSAs	1581.30	5724.51	587.74	37.17%
Recruits *Galeus melastomus*	GSA 10	900.16	3455.82	37.47	4.16%
	GSA 11	663.45	317.94	0.00	0.00%
	GSA 18	74.96	1482.34	0.00	0.00%
	GSA 19	not available	468.41	not available	0.00%
	All GSAs	1638.57	5724.51	37.47	2.29%

was possible to infer the size of the colonies from the basal diameter (Andrews et al., 2002). In particular, in both GSA 10 and GSA 18, the basal diameter distribution showed a peak at 1.5 mm. A wider range of sizes and a distribution skewed towards larger/older colonies was observed in the Southern Adriatic, while a very low percentage of colonies with basal diameters of over 2 mm was found in the South-Central Tyrrhenian (negative skewness). These differences could be the result of different anthropogenic impacts, considering that larger diameters correspond to older colonies. While reporting the presence of pristine coral gardens including IF, Bo et al. (2015a,b) observed an average colonies height of 36 cm, which corresponds to a BD of about 4 mm according to the BD-HC relationship computed in the present work. This size corresponds to the second modal component of the DFD in GSA18. Despite the little amount of morphometric data available, they seem in agreement with the same data reported in literature for other Mediterranean areas (Bo et al., 2015a; Mastrototaro et al., 2017; Mytilineou et al., 2014).

No studies on *I. elongata* age and growth have been published to date; however, a low growth rate has been reported for congeneric species. Age and growth estimates using ^{14}C have indicated maximum *Isidella* spp. ages of 75–126 years in the Gulf of Alaska (Roark et al., 2006). For *Isidella tentaculatum*, Andrews et al. (2002) estimated a slow growth rate of 0.1 mm/year and a long lifespan of about 50 years in the Gulf of Alaska. These data indicate an impact recovery period ranging from a few decades to one century for IF. However, to fully understand the recovery potential and long-term population dynamics, more

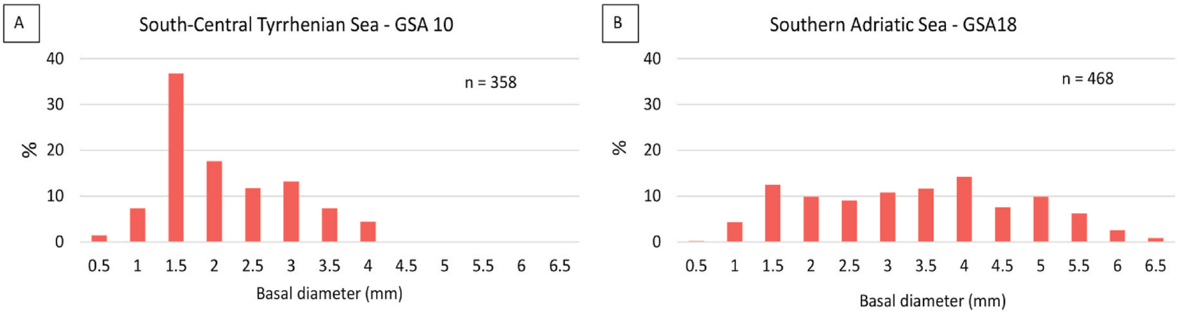

Fig. 8. Basal diameter frequency distribution of the colonies of *I. elongata* in (A) the South-Central Tyrrhenian Sea (GSA 10) and (B) the Southern Adriatic Sea (GSA 18).

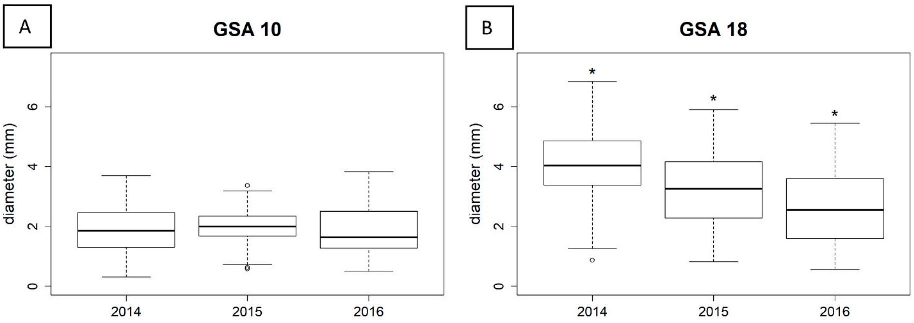

Fig. 9. Box plots of the colony basal diameters measured in the years from 2014–2016 in (A) GSA 10 and (B) GSA 18. The asterisks (*) indicate significant differences between years (Kruskal–Wallis test, $p = 6.276e^{-16}$).

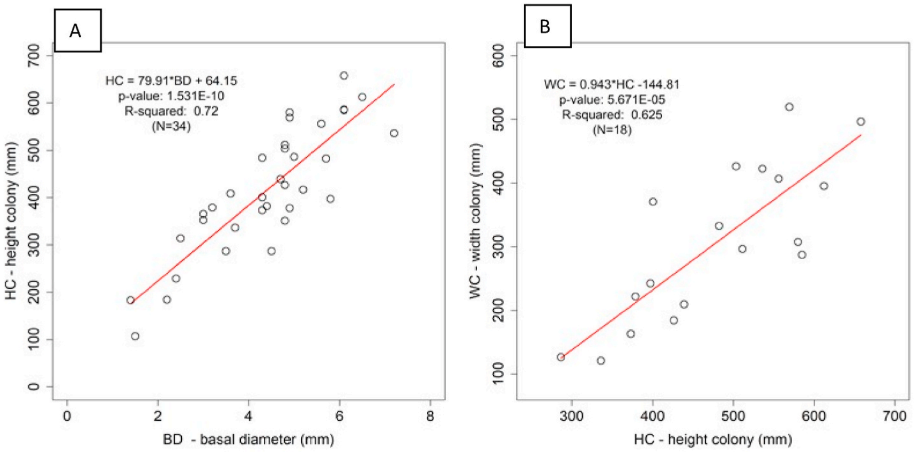

Fig. 10. Linear regression of basal diameter with height colony (A) and height colony with width colony (B). The regression equation, p value, determination coefficient (R-squared), number of colonies (N) are also reported.

information is needed about the growth rate and age of *I. elongata* in the Mediterranean basin. Other biological parameters, such as fecundity and recruitment, can support these studies, but they remain undescribed thus. Nevertheless, a significant decrease in the median basal diameters over three years could be a warning sign of degradation of IF in the Southern Adriatic, where it seems to have been less impacted than in other areas.

Like other corals, *I. elongata* is a passive feeder. Therefore, the presence of a large population is often associated with a strong presence of zooplankton (Cartes et al., 2013). These concentrations of prey at low levels of the food web could trigger a cascade of effects that could modify the fauna associated with the IF in qualitative and quantitative terms (Cartes et al., 2013; Mastrototaro et al., 2017; Rueda et al., 2019). Indeed, it is known that the macrofauna associated with cold-water coral (CWC) habitats in the Western Ionian Sea (mostly structured by *Lophelia pertusa* and *Madrepora oculata*) consists of relatively high densities of reproducing individuals and juveniles of several species (Capezzuto et al., 2018; D'Onghia et al., 2010, 2012; 2016; Sion et al., 2019), representing a biodiversity hotspot in the bathyal environment (Mastrototaro et al., 2010; Tursi et al., 2004). The study of CWCs suggests a correlation between habitat complexity created by the corals and species diversity, especially in bathyal habitats (Rueda et al., 2019) that are relatively homogeneous with limited diversity of habitat-forming species (Gage and Tyler, 1992). In our study, the comparison between assemblages in terms of biodiversity and biomass associated with the presence of *I. elongata* (ANOSIM test) showed significant differences only in GSA 18, which is less impacted by fishing activities on deep muddy bottoms. We do acknowledge the limits of the sampling gear, as already mentioned above, since the presence of a few fragments of colonies could be misleading in the identification of real IF. For this reason, only hauls carried out on muddy (preferable bottoms of this species) with a probability of occurrence greater than 80% (find at least for 4 surveys) were considered representing the IF. Indeed, we can infer that the ecological function of IF exhibiting well-developed associated communities can be fully expressed in mature populations, such as those observed in the Southern Adriatic Sea, rather than in populations consisting of younger and smaller colonies and possibly recovering from recent disturbances. It seems that only those IF showing a high level of integrity and three-dimensionality created by the bamboo coral colonies can possibly act as biodiversity hotspots (Cartes et al., 2013; Mastrototaro et al., 2017; Mytilineou et al., 2014). Conversely, IF strongly impacted by trawling consists of few and small isolated colonies (Mastrototaro et al., 2017; Pierdomenico et al., 2018), which do not constitute sufficiently attractive refuges for either spawners or juveniles of several species.

In GSA 18, the oviparous shark *G. melastomus* is the species that most characterizes the assemblage associated with *I. elongata*, as observed in the Eastern Ionian Sea (Mytilineou et al., 2014) and in the Balearic Sea (Mastrototaro et al., 2017). The three-dimensional habitat created by the bamboo coral branches constitutes an ideal habitat for the oviparous shark, supporting its egg capsules during embryonic development (Mastrototaro et al., 2017). The strong presence of Aristeidae (*A. foliacea* and *A. antennatus*) associated with the IF has been reported in several areas of the Mediterranean (Cartes et al., 2013). This association could be explained by the presence of Pandalidae species, the favourite prey of both *A. foliacea* and *A. antennatus* (Kapiris, 2012). The presence of Pandalidae, such as *Plesionika martia*, *Plesionika heterocarpus* and *Plesionika giglioli*, seems to be linked with the high concentration of copepods in the IF (Cartes et al., 2013). However, it is unclear whether the Pandalidae species are associated with the IF habitat or only share trophic conditions with the corals, such as wide zooplankton availability (Cartes et al., 2013). At any rate, the high concentration of pandalids and other crustaceans, such as Pasiphaeidae, attracts predators of several levels and, besides the above-mentioned Aristeidae, bony fishes (e.g. *H. mediterraneus*, *M. merluccius*, *P. blennoides*, *H. dactylopterus*), elasmobranchs (e.g. *Etmopterus spinax*, *Scyliorhinus canicula*, *Dalatias licha*) and ommastrephid cephalopods (e.g. *Illex coindetii*, *Todarodes sagittatus*, *Todaropsis eblanae*). Most of these species (*A. foliacea*, *A. antennatus*, *M. merluccius*, *P. blennoides*, Ommastrephidae) are of high commercial value. Moreover, the cascading effects on the bottom in terms of energetic flow, which are triggered by the presence of the IF, are the reason for the high presence of species such as *Pagellus bogaraveo*, *Coelorinchus caelorhincus, Nezumia aequalis* and *Nezumia sclerorhynchus*, which preferentially prey on benthos (polychaetes and/or ophiuroids) (Cartes et al., 2013; Mastrototaro et al., 2017; Mytilineou et al., 2014).

An Essential Fish Habitat (EFH) is defined as the preferential area/habitat where fish perform their most important vital functions, such as spawning, breeding and feeding. From a management point of view, these habitats require particular protection and management actions to guarantee sustainable exploitation of the relevant stocks, especially those identified as GFCM priority species (GFCM, 2018). CWC frameworks have been identified as EFHs (Capezzuto et al., 2018, 2019; D'Onghia, 2019; Sion et al., 2019) mostly due to their importance in the reproductive phase of such species as *G. melastomus*, *Conger conger*, *H. dactylopterus*, *M. merluccius*, *P. bogaraveo* and *P. blennoides* (Capezzuto et al., 2018; D'Onghia et al., 2016). The role of the IF as an EFH has only been partially explored (Cartes et al., 2013; Mastrototaro et al., 2017; Maynou and Cartes, 2012; Rueda et al., 2019), with a documented functional linkage in spawning for oviparous elasmobranch species, such as *G. melastomus* and *S. canicula*. While such interactions have already been documented, quantitative analyses of the actual ecological role of the IF are still lacking, even though Cartes et al. (2013) noted a rather limited capacity of the IF to form a habitat for megafauna.

The analysis performed in our study confirms that deep-dwelling oviparous shark species can benefit from the IF, most likely where this habitat is less impacted and thus has a more complex canopy. Egg capsules of *Scyliorhinus* spp. have been identified anchored to the branches of *I. elongata* in the Balearic Sea (D'Onghia, 2019; Mastrototaro et al., 2017) beside other structuring species, such as the black coral *Leiopathes glaberrima* (Cau et al., 2017). In GSAs 10 and 18, where IF seems to be more present, the spawning grounds of *A. antennatus*, *A. foliacea* and *G. melastomus* and the nursery areas of *A. foliacea* exhibit a high level of overlap with the bamboo coral habitat. In contrast, the nursery areas of *G. melastomus* display a low level of overlap. This is related to the ecology of this species, with juveniles generally distributed in a wider depth range than that of the IF (Ragonese et al., 2009; Rey et al., 2005; Tursi et al., 1993) and adult individuals mostly segregated deeper than 400 m (Tursi et al., 1993).

5. Conclusion

The assessment of VME distribution and their use by fish and invertebrates is of extreme importance for the implementation of effective management and conservation measures. An ecosystem approach to fishery management should include spatial considerations and integrate the protection of vulnerable and sensitive habitats as an emerging issue (Caddy, 2014; D'Onghia et al., 2019). The mapping of *I. elongata* presence allowed us to identify hotspots with a higher probability of IF presence in trawlable areas. This input is very important for implementing appropriate measures both to further investigate these habitats with suitable techniques and to preserve their ecological function. Indeed, this study highlights differences in terms of biodiversity and species assemblages associated with the IF, mostly in areas where the latter are less impacted. It also highlights the role of the bamboo coral habitat as an EFH for different life stages (adult and/or juvenile) of various species (*A. foliacea*, *A. antennatus*, *G. melastomus*). The need to protect the identified areas is also confirmed by the increasing signs of impact on the bamboo coral facies. This outcome can be very informative from a management perspective for implementing appropriate spatial measures aimed at preserving the ecological function of this key coral species.

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.

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