



The macrofauna associated to the bamboo coral *Isidella elongata*: to what extent the impact on isideidae affects diversification of deep-sea fauna

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Abstract Macrofauna associated with the bamboo coral *Isidella elongata* was analysed in the Balearic Basin at depths of 697–1308 m. The diversity of associated macrofauna and the specific associations identified depended on different morphological characteristics of colonies, such as height or density of rami. Species associated with *Isidella* consisted mainly of sessile fauna, such as cnidarians (the actinian *Amphianthus dornhii* and the solitary coral *Desmophyllum dianthus*) and cirripeds (*Gibossaverruca* sp.). The strongest relationship (commensalism) occurred for the Pontogeneiidae amphipod *Dautzenbergia megacheir*, living attached to colonies of *Isidella* and represented by all population stages from adult (oostegal) females and males to juveniles. Species-coral relationships between *Dautzenbergia* and bamboo corals (Isididae) are plausible. *Dautzenbergia* spp. showed morphological differences between Atlantic (described by Walker 1897 as “eyes wanting”) and Mediterranean (with well-developed reddish eyes) specimens. This would suggest diversification of this genus, as has been recently suggested for Pleustidae associated with deep gorgonians. The diversity of the macrofaunal community associated with *I. elongata*

was higher in the most mature (larger colonies with higher density) fields found NW of Mallorca, with higher colonies than in other parts of the Mediterranean. This was the only site where *Gibossaverruca* sp. (a first Mediterranean faunal record) and *D. dianthus* were collected. These complex associations between macrofauna and deep-water corals may provide arguments to protect these fragile ecosystems as a source of faunal diversity and diversification.

Keywords Deep corals · Associated fauna · Deep sea · Amphipods · Diversification · Vulnerable species

Introduction

Isididae, known as bamboo corals, are widely distributed worldwide in deep waters at depths mainly between 200 and 1500 m depth and deeper to 2250 m and abyssal depths (Morris et al. 2012). *Isidella elongata* is the only species of bamboo coral regularly reported in soft bottoms in the deep Mediterranean (Dieuzeide 1960; Maynou and Cartes 2012; Cartes et al. 2013; Carbonara et al. 2020). The case of this species, here analysed, cannot be considered as local, but is extrapolable to wide deep sea areas, all over the world, where we found other isidids. In the Balearic Basin, the species occupy bathyal depths (Maynou and Cartes 2012; Cartes et al. 2013), with some citations at depths as shallow as 48–60 m on the Catalan coast (Gili et al. 1987). Among the 138 described species of Isididae, most have the capacity to form specific-species fields or gardens (Watling and Auster 2005; Buhl-Mortensen and Mortensen 2004) on soft-bottom sediments. *I. elongata* colonies have a two-dimensional tree or bush form that, combined with its moderate size and the spaced way in which colonies appear distributed in these fields, constitute

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a less compact habitat for possible associated fauna compared with those generated by hard corals or Gorgoniidae. Gorgoniidae generate more three-dimensional reef structures and generally form more aggregated or dense fields than *Isidella*. In this way, gorgonians can form more *forests*, a term adopted from terrestrial/human landscapes, whereas bamboo coral *forests* (Krieger and Wing 2002) have a structure more similar to an open savannah, based on in situ images (Mastrototaro et al. 2017; Pierdomenico et al. 2018).

Habitats generated by deep gorgonians, sea pens and similar taxa are not well studied, especially in the deep Mediterranean. These species form more or less dense aggregations and can become dominant in their habitat, generating different conditions from those surrounding them (Torriente 2020). One of the characteristics that modifies the prevailing spatial conditions is the increase in three-dimensional complexity. On soft-sedimentary, homogeneous bottoms, sessile colonial organisms (not only cnidarians but also sponges) are important for generating such complexities, enhancing marine diversity at mesospatial scales by increasing ecological niche dimensions (Gage and Tyler 1991). Such habitats generated by corals are home for mobile crustaceans and by other invertebrates (Fujita and Ohta 1988; Buhl-Mortensen and Mortensen 2004; Baillon et al. 2014; De Clippele et al. 2015) that use corals as a substrate for attachment, as refuge or for more intense relationships such as feeding (Burkepile and Hay 2007; Rodríguez-Romeu et al. 2016). Some of these species are cited as commensals of corals (Taboada et al. 2019), although details of most of these relationships are poorly understood.

This capacity to generate habitat for deep-cold corals has been studied by video of in situ images (D'Onghia et al. 2010; Mastrototaro et al. 2017; Pierdomenico et al. 2018; de la Torriente et al. 2020) but is also based on trawling data (Colloca et al. 2004; Maynou and Cartes 2012; Cartes et al. 2013). Studies have mainly focused on megafauna (fish and large invertebrates), and much less on macrofauna (Buhl-Mortensen and Mortensen 2004; De Clippele et al. 2015). In both cases, a high number of species seem to appear associated with corals (Colloca et al. 2004; D'Onghia et al. 2010; Maynou and Cartes 2012; Rueda et al. 2019), which have some advantages that may favour their distribution, density or some aspects of their life history (spawning or recruitment). Video images have an obvious advantage in that they are not intrusive, i.e. colonies/fields are not destroyed or removed from the seafloor. In contrast, trawling information removes corals from their habitat and conflates the fauna from coral fields with adjacent patches that may not have corals. This happens because the natural distribution of bamboo corals is not homogeneous but patchy with suitable and

unsuitable areas distributed within the same depth range (González-Irusta et al., unp.). On the other hand, the number of megafauna species (fish and decapods) truly associated with *I. elongata* in the deep Mediterranean is very low (Cartes et al. 2013; Rodríguez-Romeu et al. 2016), which seems related to the morphology of their colonies but is also influenced by the general impoverishment (oligotrophy) of deep Mediterranean fauna compared with neighbouring Atlantic waters. In fact, although some isidid species have colonies reaching up to 3 m in height (Krieger and Wind 2002), the height of Mediterranean colonies hardly exceeds 60 cm. Moreover, in addition to increasing diversity, the *I. elongata* facies can also enhance the density of associated fauna, as seems to be the case for the deep-water shrimp *Aristeus antennatus* and *Plesionika martia* (Maynou and Cartes 2012; Ragonese 2018), although more studies are needed to disentangle the common distribution of species in the same depth ranges from the capacity of corals generating habitat for these species.

Some rather scarce studies have attempted to identify the level of these associations for macrofauna demonstrating how, among amphipods, some families such as Pleustidae seem specialized in living as commensals on gorgonians (Bellan-Santini et al. 1993; Myers and Hall-Spencer 2004; Schwentner and Lörz 2020). Because of technical limitations, these small species (ranging between 1 and a few mm) are often not captured by images, especially mobile (e.g. epibenthic-suprabenthic) species or, if observed, classification is not specific. The collection of corals by trawling is accidental, but when it occurs, it gives us the opportunity to identify macrofauna, both sessile fauna living on coral structure or epibenthic mobile organisms living on rami or associated with polyps. Additionally, it is possible to establish strong relationships between macrofauna and corals, which is information that is very scarce compared with abundant megafauna “associated” with corals. In comparison to deep-water corals in the subclass Hexacorallia, the capacity of Isididae to form essential habitats for other organisms is poorly known (Fosså et al. 2002; Krieger and Wind 2002; Metaxas and Davies 2005).

Despite its relatively deep and disperse distribution in the Mediterranean, *I. elongata* is threatened by human activities, especially deep-sea bottom trawling (Cartes et al. 2017; Pierdomenico et al. 2018). Similar to other long-lived, filter-feeding and habitat-forming species, *I. elongata* is very sensitive to trawling impacts (Pierdomenico et al. 2018), and its population is critically endangered in some Mediterranean areas (Gerovasileiou et al. 2019). In fact, *I. elongata* aggregations are a vulnerable marine ecosystem (VME) according to the FAO definition (FAO 2009) and have been included by the General Fisheries Commission for the Mediterranean (GFCM) on the list of

sensitive habitats (GFCM 2009). The removal of this species can also affect a number of species that live associated with bamboo corals. Establishing the intensity of these relationships can help to determine to what extent human impacts affect the diversity and diversification of deep habitats.

Our objectives in this study are: (1) to identify the sessile and mobile macrofauna associated with *I. elongata* in the Balearic basin; (2) to establish to what extent the corals have the capacity to generate an essential habitat for each of these species; and (3) to catalogue as far as possible the degree of dependence between the different species found over/close to bamboo corals, e.g. relationships of commensalism.

Methods

Study area and sampling

The sampling area comprised the slopes of the Balearic Basin (western Mediterranean) between the coasts of Catalonia and to the north of the Balearic Islands (Fig. 1). The Balearic Basin, one of the largest in the Mediterranean Sea, occupies an extense area of ca. 68,500 km². From 1985 to 2020, periodic cruises were performed at depths between 200 and 2300 m isobaths (Cartes et al. 2015 and references included therein), with a total of 237 bottom trawls performed covering ca. 14.8 km² of the seafloor. More than 90% of trawls were performed using a single model of trawl, the OTSB-14 (Merrett et al. 1991), and on the same

R/V (R/V García del Cid). During ANTROMARE0611 (18–25 June 2011), the R/V was the *Sarmiento de Gamboa*.

Colonies of *I. elongata* were accidentally collected in 27 trawls, while dead remains (bases and/or with first segments of the colony stem) were collected in another 22 hauls. To date, it is very unpredictable where *Isidella* can be found and removed from the bottom, since its distribution is not only dependent on an optimal depth but driven by several factors generating a patchy distribution in the area (González Irusta et al., unpubl.).

Corals and associated fauna

Since the 2007 cruises, colonies were counted and weighed, and size (height) was also recorded. In addition, different measurements were collected in the laboratory: (1) the diameter of the nearest segment to the first bifurcation of the stem (often it is the 3rd segment, although the stem can have 4–5 or even 7 segments/rings) and the 1st segment (the closest to the colony base) when it was present (often cut by trawling); and (2) the number of rami of colonies counted for well-preserved specimens at the point where colonies showed their greatest width.

For epibiont analyses, colonies were visually analysed on board and in the laboratory, and sessile epibionts were identified and counted. In the laboratory, colonies were washed with water, individually or in groups of 3 maximum; the water collected in a bucket with colony remains was sieved through a 200 µm filter to recover mobile epibionts (basically peracarid crustaceans) in the macrofauna. Species were sorted under a stereomicroscope (X10-

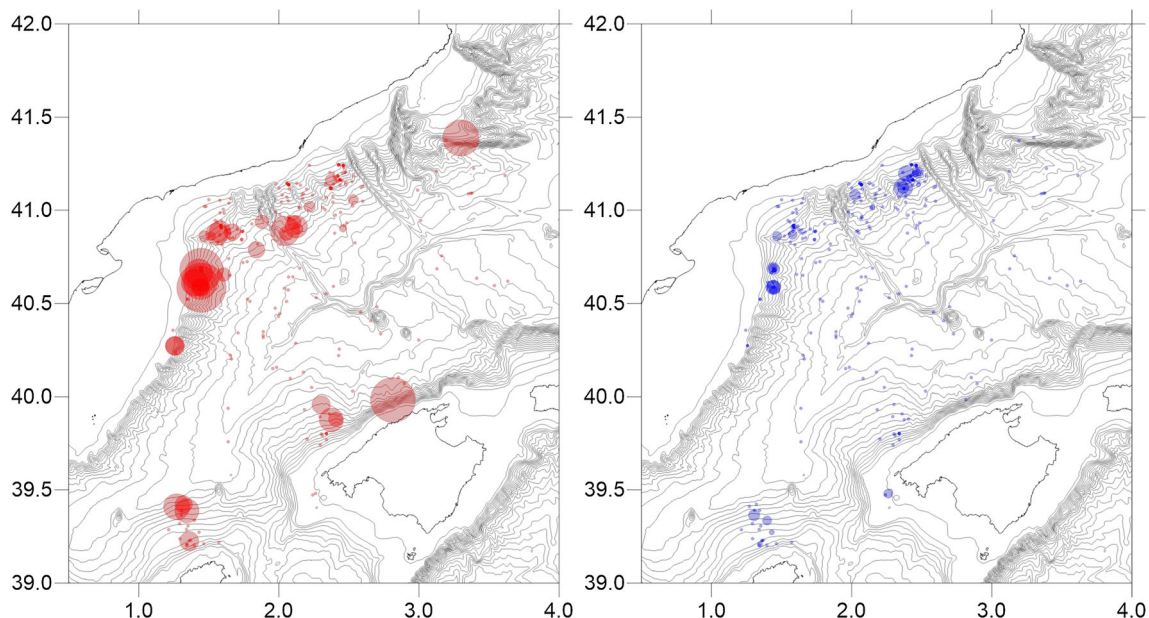


Fig. 1 Map of the Balearic Basin, showing all the sampling performed between 1985 and 2020 (OTSB14 bottom trawls) and the distribution of *I. elongata*; (red circle) alive colonies (map at left); (blue circle) dead colony remains or bases (map at right)

X40), identified to the lowest taxonomic level, listed, counted and assigned to each colony. The distribution of the most widely distributed species was mapped (individuals/colony).

The majid crab *Anamathia rissoana* was often captured in association with *Isidella* catches (Mura et al. 2005; Cartes et al. 2013). The stomach content of 5 specimens collected in a field of bamboo coral found NE of Mallorca (see below) was also analysed. Individuals were measured and dissected, and their gut content was examined under a stereomicroscope at X10–X40 and prey were classified to the lowest possible taxonomic level.

Data analyses

The diversity of macrofauna associated with *I. elongata* was calculated by three of the most widely used indexes (S , H' and J , Magurran 2013) on the 3 types of *Isidella* fields ($f1$, $f2$, and $f3$, see Fig. 2) for post comparisons. Species richness (S), the simplest measure of diversity, consisted in a count of the different species inhabiting each *Isidella* field. The Shannon (H') and Pielou (J) evenness measures are considering also the abundance of each species, but J is in addition measuring how equal is the contribution of each species in its community. The combination of these diversity measures give us a more complete view about

how a community is structured. The 3 fields corresponded to (1) a dense (mature from an ecological point of view) field of bamboo coral found NW of Mallorca; (2) sparse colonies collected in a number of hauls throughout the basin at depths > 1000 m; and (3) some small (likely regenerating) colonies found SE of the Ebro Delta. The size frequency of colonies (segment ϕ of the most basal first segment, $S1$) in the 3 areas was constructed, and the density of colonies (specimens per swept area, ha) was calculated. We also added partial information on a 4th field NE of the Ebro Delta, characterized as optimal habitat for *I. elongata* in the middle slope (620–670 m), but since the end of the 1990s, it has been highly impacted by trawling (Cartes et al. 2013).

The relationships between the more distal (closer to the first bifurcation of the colony) segment ϕ vs the most basal (closer to the colony base) segment ϕ ($S1\phi$) were established for *I. elongata* colonies in the Balearic Basin (Figure S1). Since colonies were often damaged and usually the base and first segments were missing, this relationships is useful in increasing the number of specimens for the size distribution of populations.

Canonical correspondence analysis (CCA) is a multivariate technique for extracting synthetic environmental gradients from a number of explanatory variables in a dataset. It is widely used for ecological studies to elucidate the relationships between species and their environment (Ter Braak and Verdonschat 1995). In our case CCA was used to establish relationships between (1) epibiont distribution/abundance and morphological characteristics of colonies and (2) epibiont abundance and some environmental variables. In CCA, ordination axes are linear combinations of environmental variables (arrows on plots), and each arrow length is proportional to the importance of each variable (Ter Braak 1986), in our case explaining the influence of the morphological characteristics of coral colonies and of environmental variables on the distribution/abundance of epibionts. Species in our CCAs were distributed according to the size and density of rami. Environmental data consisted of T , S , turbidity, fluorometry and oxygen (O_2) recorded in the near bottom (5–10 m above the bottom) by CTD profiles performed at each station. Mean values for each variable were calculated, and the sensors attached to the CTD recorded 24 data/sec (see details in Cartes et al. 2015). T and S were highly correlated; therefore, T was not considered in the CCA presented here.

In addition to CTD data, the variable current intensity (in m/s) at each sampling site was added. Current intensity (CI) was extracted from the model “Mediterranean Sea analysis and forecast” (Clementi et al. 2019) and computed following the next formula:

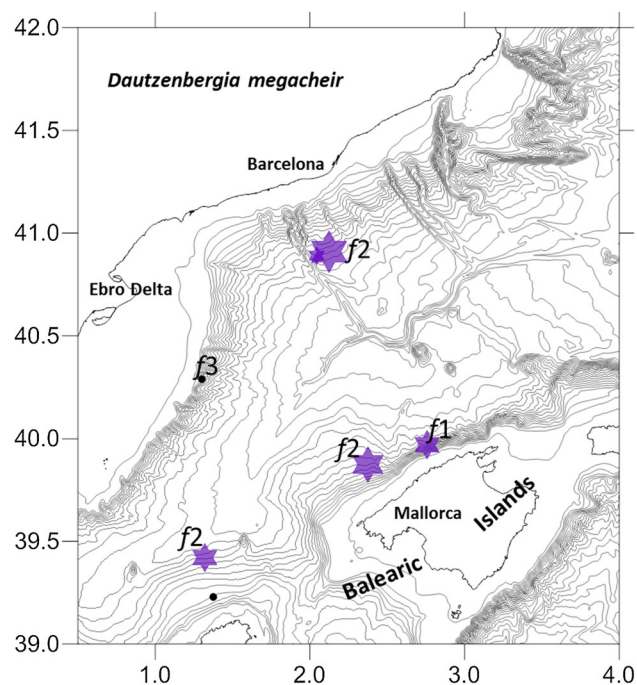


Fig. 2 The distribution of *D. megacheir* associated to *I. elongata* colonies in the Balearic basin, in samples performed between 2011 and 2020. Dots are proportional to species abundance. $f1$ represented dense (mature) fields of bamboo coral, $f2$ fields with sparse (large) colonies, and $f3$ fields with small (likely regenerating) colonies

$$CI = \sqrt{(U^2 + V^2)}$$

where U is current velocity in the x axis (U velocity) and V is current velocity in the y axis (V velocity). The final layer was resampled from the original resolution to the final resolution of 2×2 km using near neighbourhood interpolation. Finally, the values of each sample for this variable were computed using the function extract from the raster package (Hijman 2020) and the coordinates of each sample. One of the designed analyses combined data sources, most of which had some trophic meaning, such as fluorometry (representing possible Chla inputs over the bottom), turbidity (resuspended matter) and current intensity. All data were log transformed. The software XLStat (AddinSoft Inc.) was used for the CCA.

Results

The size frequency of *Isidella* colonies was quite different at the 3 fields established (Fig. 3). At $f1$ (mature field) we found the largest colonies (to 12 mm ϕ of S1; modal size = 7 mm ϕ). At $f2$ we found also large colonies, ranging between 5 and 9.5 mm S1 ϕ , while at $f3$ colonies were very small (0.5–1 mm). At the NE of Ebro Delta field, in spite we found dense aggregations of *I. elongata* indicating an unaltered habitat, the size of colonies were rather moderate (1–4.5 mm ϕ of S1. The density of bamboo coral found NE of Mallorca ($f1$) was 28.5 colonies/ha; the density in the area with sparse (large, well-formed) colonies at depths > 1000 m ($f2$) ranged between 0.2 and 0.6 colonies/ha; while SE of the Ebro Delta, the density of small regenerating colonies ($f3$) was 1–2.3 colonies/ha. North of the Ebro Delta, density in an area with a high density of

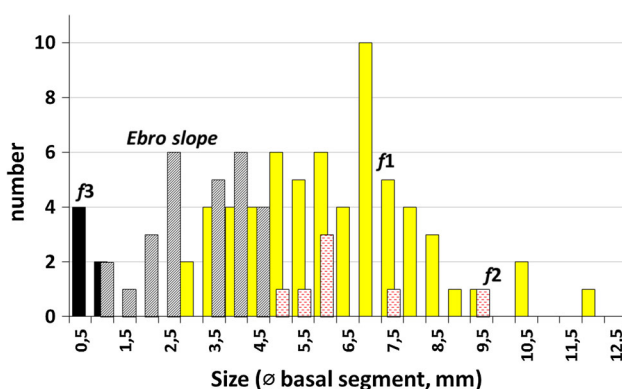


Fig. 3 Size distribution of *I. elongata* in different areas of the Balearic Basin (1st basal segment ϕ , in mm), from colonies collected by trawling. As in Fig. 2 legend $f1$ are mature fields, $f2$ fields with sparse colonies and $f3$ small regenerating colonies. Size distribution for an Ebro slope field added

colonies that were very small to medium sized, density was (in 1994) between 15.4 and 479 colonies/ha at 626–670 m.

Nine species, 8 of which were macrofauna, were identified, with different degrees of association with *I. elongata* colonies (Table 1). We excluded species clearly belonging to the zooplankton that were sporadically found when the remains of colonies – after washing and sieving – were sorted, considering that they were pasted in the codend of the OTSB14 trawl with the rest of the capture. Examples include the siphonophore *Chelophyeas appendiculata*, the scyphozoan *Peryphilla peryphilla* and the euphausiid *Nematoscelis megalops*. The calanoid *Candacia tenuimana* (Table 1) probably had the same origin.

In the list, we included the majid *Anamathia rissoana* (large macrofauna, in fact) with 5 specimens captured in the northeastern Mallorca field analysed for gut contents (see below).

Among mobile peracarid species, practically all specimens collected (164) were *Dautzenbergia megacheir* (Pontogeneiidae) collected in both dense fields of bamboo coral NE of Mallorca and in sparse (large) colonies collected in different hauls throughout the basin at > 1000 m (Fig. 2; Fig. 4). No specimens were collected in the area SE of the Ebro Delta, which had small colonies that were apparently regenerating, while no data from colonies in 1994 from NE of the Ebro Delta were available. The Sebidae *Seba aloe* was represented by 5 individuals that were also collected in the northeastern Mallorca field and in the station formed by sparse colonies at > 1000 m in the Balearic Basin. The isopod *Ilyarachna* cf. *antarctica* was represented by a single individual.

Sessile fauna were also represented by Crustacea; in this case, cirripeds belonging to Verrucidae were collected in high numbers in the dense (mature) field NW of Mallorca (Table 1). The specimens belong to *Gibossaverruca* sp., which is a new genus in the Mediterranean (deep-sea) fauna (Fig. 4).

Additionally, among sessile epibionts, the small sea anemone *Amphianthus dornii* was found attached to the rami of *I. elongata* in all areas sampled, including the small regenerating colonies SE of the Ebro Delta. The solitary coral *Desmophyllum dianthus* was found only in the northwestern Mallorca field.

Serpulidae tubes were attached to colonies NE of Mallorca, and in sparse colonies at > 1000 m, and tubes belonging to the genus *Spirobranchus* sp. with 1 alive specimen were found at an isolated colony (A1-17, 996 m, N of Mallorca, 39° 52.599 N–2° 18.030 E). Hydrozoa, represented by reptant colonies (Leptothecata) attached to some coral remains, were sometimes present, but it was not possible to count them and they often seemed represented by empty tube structures.

Table 1 List of alive fauna associated to *I. elongata* in the Balearic Basin, with number of epibionts in the three areas with *I. elongata* established (mature forest, sparse colonies and regenerating colonies)

	Ne mallorca Mature field	Balearic basin Sparse colonies	SE Ebro delta Regenerating
Polychaeta			
Serpulidae (tubes)	14	2*	0
Cnidaria			
<i>Amphiantus dornhii</i>	87	50	2
<i>Desmophyllum dianthus</i>	12	0	0
Crustacea			
Cirripeda			
<i>Gibossaverruca</i> sp.	95	0	0
Peracarida			
Amphipoda Gammaridea			
<i>Dautzenbergia megacheir</i>	151	13	0
<i>Seba aloe</i>	4	1	0
Isopoda			
<i>Ilyarachna</i> cf. <i>antarctica</i>	1	0	0
Copepoda calanoidea			
<i>Candacia tenuimana</i>	1	0	0
Decapoda			
<i>Anamathia rissoana</i>	5	0	0

Serpulidae are empty tubes exceptuating * (*I. spirobranchus* sp.). One tube in NE Mallorca corresponded to *Apomatus* sp.

Epibiont versus *Isidella analyses*

Diversity (S , H' and J) indices were calculated for the associated macrofauna for the 3 established fields. The number of species (S) was 9 in the mature field NW of Mallorca, 4 in the zone with sparse colonies and only 1 epibiont (*Amphiantus dornhii*) was found in the regenerating area. The Shannon (e) diversity (H') was 1.34 NW of Mallorca, 0.70 in the sparse colonies and zero in the regenerating area. The highest evenness (Pielou's J) was recorded in the NW of Mallorca (0.609) and it was 0.505 in the sparse colonies field. At the regenerating area, with a single epibiont counted, it was not possible to calculate J .

The CCA performed on the hauls taken at the three established stations (see above) related the highest portion of sessile epibionts, especially the cirriped *Gibossaverruca* sp. and the coral *D. dianthus*, mostly with dead colonies, those remains formed by the base, the stem and some rami devoid of polyps, and thus they appeared associated in the CCA to the variables "no polyps", low number of rami, and reduced (colony) size (Fig. 5). Although the colonies that appeared attached were in origin large, the remains measured with these epibionts were < 20–25 cm. Serpulids were also found on some live colonies, while the sea anemone *Amphianthus dornhii* was always found on live colonies in the middle and upper parts of colonies (20–30 to 60 cm above the sea bottom) but not necessarily on large

colonies or colonies with a high density of polyps, hence its position in the CCA. The two mobile peracarids, the amphipods *D. megacheir* and *Seba aloe*, were collected (after washing colonies) in colonies that were very large, with a high density of rami (and polyps); therefore, both species occupied an opposite place in the CCA compared with the distribution of sessile epibionts. Since no in situ data are available, we cannot establish (for the sea anemone) if the species had some requirements for occupying the low, middle or upper levels on the corals.

The CCA performed with environmental variables (Fig. 5) demonstrated how the cirriped *Gibossaverruca* sp. and the coral *D. dianthus* were linked to stations with higher near-bottom fluorescence (likely particulate marine snow), less turbidity and lower current intensity. Since these organisms appeared on dead remains, at or close to the stem of colonies, they could avoid turbid waters with resuspended matter. In fact, they only appeared in the insular stations. In contrast, the sea anemone *Amphianthus dornhii* was found to be mainly linked to high turbidity in the CCA, probably exploiting more resuspended matter. The two mobile peracarids, the amphipods *D. megacheir* and *Seba aloe*, were not clearly associated with any variable in the CCA. In fact, *D. megacheir* was distributed both over the mainland and insular sides of the Balearic Basin (see map).



Fig. 4 Images of the two autochthonous associated species of *I. elongata*, the amphipod Pontogeniidae *D. megacheir* (male and female) and the cirriped *Verrucomorpha* sp. Both corresponded to fresh specimens

Discussion

Although diversification based on phenomena of adaptive radiation is well known in marine habitats, including fauna associated with cnidarians (e.g. between clownfish and anemones, Litsios et al. 2012; between nudibranchs and corals, Fritts-Penniman et al. 2020), similar interactions with deep corals (also able to generate essential habitats for associated species) are practically unknown with few exceptions (Chimienti et al. 2020). In most cases, these associations are not fully established and are interpreted as *casual* associations between species after trawling wide areas (with and without corals) or by recording images (D'Onghia et al. 2010; Mastrototaro et al. 2017). In addition, commensalism is, with few exceptions, the strongest interaction documented in deep-sea corals (Chimienti et al. 2020), likely a weaker cause of possible diversification than mutualism (Litsios et al. 2012). It is not obligatory that a definite species associated with corals may maintain these associations throughout its entire life cycle, and biological stages of a species can derive some benefit in coral fields for reproduction (spawning or recruitment), as a refuge for juveniles or for trophic relationships. In this way, it seems

logical that the refuge effect is higher in corals with a higher density of colonies and 3D structure, characteristics that *Isidella* does not completely fulfil. The higher abundance and larger size of some commercial fish in *Lophelia pertusa* reefs compared with surrounding areas seems related to higher food availability in the reefs (Husebø et al. 2002), but such a possible trophic link has rarely been established. In bamboo coral habitats of the western Mediterranean, we identified *Notacanthus bonapartei* feeding on *I. elongata* polyps (Rodríguez-Romeu et al. 2016). Another trophic link was observed for the majid *Anamathia rissoana*, with the occurrence in their stomachs of *Isidella* sclerites, which is similar to some nudibranchs (Chimienti et al. 2020) documented to be associated with *Callogorgia* corals in the deep Mediterranean. In the case of majids, they seem to feed on the organic parts of colonies that wrap rami. *Anamathia rissoana*, however, was not only collected from *Isidella* fields (Mura et al. 2005; Cartes et al. 2013; Mastrototaro et al. 2017), but was cited as associated with other deep gorgonians (Dieuzeide 1960; Mura et al. 2005; Lee et al. 2020; including *Lophelia pertusa*: Carlier et al. 2009) in the Mediterranean, and was collected by trawling at 301 m, together with the sea-pen

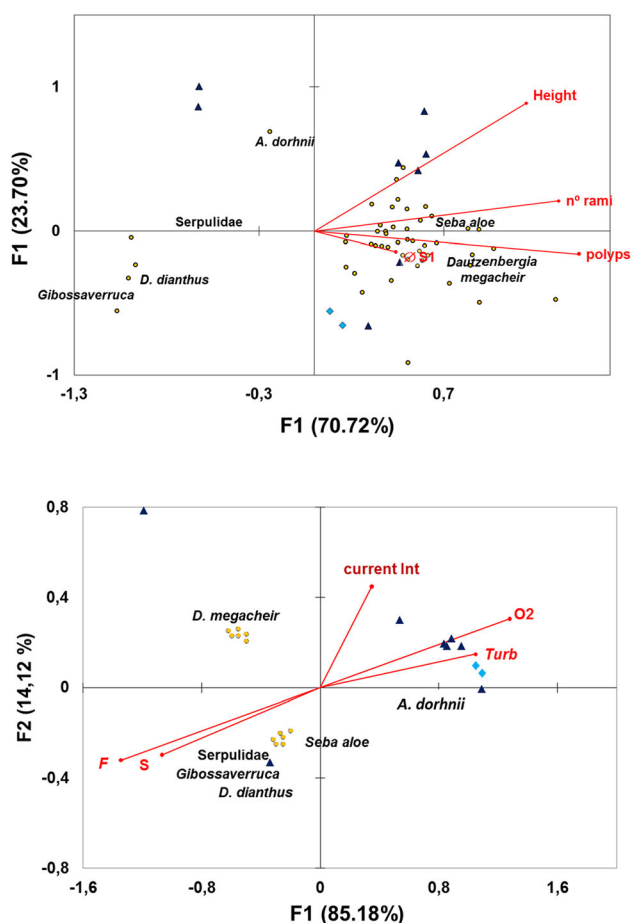


Fig. 5 Relationship between epibiont associated macrofauna and morphological characteristics of *I. elongata* colonies in the Balearic Basin with some geographical variables. Results based on a Canonical Correspondence Analysis, CCA. Morphological features are: 1st basal segment \emptyset , in mm, colony height (cm), no of rami/colony; occurrence of polyps in the colony (0, 1). Environmental variables were near bottom salinity (S), fluorescence (F), oxygen (O₂) and turbidity (Turb), and current intensity. Yellow points are colonies from mature fields (f1), triangles and diamonds from sparse colonies fields (f2)

Funiculina quadrangularis (author's unpubl. 2003 MEDITS cruise).

It is well known how *Primnoa* spp. and *Lophogorgia* spp. generate habitat for small macrofauna (mainly amphipods: Buhl Mortensen and Mortensen 2004; Schwentner and Lörz 2020). The conditions that corals may create (Krieger and Wing 2002; Metaxas and Davies 2005) may generate different levels of relationships for species living on or near them. Among anomuran decapods, there are diverse (macro) fauna associated with cold-water corals (*Lophelia pertusa* or gorgonians) on the Galicia Bank (Cartes et al. 2014), with no less than 6 galatheid (*Munidopsis* spp., *Uroptychus* spp.), chirostyliid (*Gastroptychus formosus*) and homolodromiid (*Dicranodromia mahieuxii*) crabs collected. *Primnoa* has a dense bush

shape and can reach a height of 2 m (Krieger and Wing 2002), while *I. elongata* has thin branches and is, at least in the Mediterranean, smaller. The only species of anomurans (*Munidopsis tridentata*) associated with a deep coral in the deep Mediterranean was found attached to *Paramuricea* sp. (Cartes 1993). In this case, in addition to the different structures and generating habitat capacities of corals (Agudo-Adriani et al. 2016), the low anomuran diversity is probably due to the particular isolation of the deep Mediterranean (see below).

The strongest interaction found in the Balearic Basin was in the amphipod *D. megacheir*, collected at different stations in the Balearic Basin and always associated with corals (164 specimens collected attached to colonies). All population stages, from adult (oostegal) females and males to a high number of juveniles, were present in our samples; therefore, the species seems to be linked to the isidid throughout its entire life cycle. These interactions for macrofauna (amphipods) have not been previously documented for *I. elongata*. *D. megacheir* has previously been collected by Cartes and Sorbe (1999) in the Balearic Basin (8 specimens) with a Macer-GIROQ suprabenthic sledge (armed with 0.5 mm plankton nets, Cartes et al. 1994) operating on the (muddy) bottom surface. Although specimens were not directly obtained from *Isidella* colonies then, colonies were also collected in trawlings performed in the same area (at 1250–1263 m) of amphipod collection (Sardá et al. 1994). For the rest of the Mediterranean, only two specimens were cited by Diviacco (1983), and recently, it was found in Capbreton (southeastern part of the Bay of Biscay) at 560 m (Frutos and Sorbe 2017). Unfortunately, the taxonomic literature rarely provides details on their ecology (habitat) (see Table S1). Although in the Mediterranean review of amphipods by Bellan-Santini et al. (1993), the species was described as “probably associated with gorgonians”, Diviacco (1983) cited only in ecological remarks “fondi fangosi batiali”. Since > 94% of Mediterranean specimens have been collected associated with *I. elongata*, the link between both species seems clear. Finally, *D. megacheir* has not been collected in association with any other deep cold coral in the Mediterranean, which reinforces a species-specific relationship with *I. elongata*.

Beyond the Mediterranean, *Dautzenbergia* species occupy bathymetric levels that can overlap with depths inhabited by other Isididae distributed from the North Atlantic to the Indian Ocean. So the case of *I. elongata* cannot be considered as local, being likely extrapolable to wide deep sea areas, all over the world, where we found other isidids. Regarding only the genus *Isidella*, a number of species are distributed in the NE Atlantic from Morocco to North Norway-Greenland (*Isidella longiflora* and *Isidella lofotensis*), *Isidella tentaculum* from northeastern

Pacific seamounts (Etnoyer 2008), *Isidella tenuis* (Cairns 2018) off of the Galápagos and *Isidella trichotoma* in the central North Pacific; all of which lack information on possible associated macrofauna. This lack of ecological information does not allow us to proceed further towards a likely hypothesis linking *Dautzenbergia* spp. with presumable speciation associated with Isididae. A recent revision of Pleustidae associated with cold corals increased – based on molecular analyses – the number of reported new species, which exhibited high endogamy (inbreeding); therefore, the authors linked the small amount of exchange with other populations with strong host specificity, since species were associated with different host gorgonian species (Schwentner and Lörz 2020). Other Pleustidae, by contrast, were more widely distributed and exhibited very low differentiation among relatively close (separated by 130 km) populations. We could have among *Dautzenbergia* spp. a case of an adaptative radiation that could be related to commensalism. The low dispersal capability of amphipods, in general by peracarids, with a direct development by embryos occurring in the oostegal bags of females would favour this. Additionally, the geographic barrier of the Gibraltar Strait (with a maximum depth of only 365 m depth) may contribute to possible isolation of the Mediterranean populations of *D. megacheir*. Most deep-sea Mediterranean endemics are distributed at deep depths (Pèrès 1985) below the maximum depth of the Gibraltar Strait; in this sense, the shallower depth limit distribution of *D. megacheir* is 600 m (Diviacco 1983). The Mediterranean populations would be different from those from the deep Atlantic. Although genetic information is not available for *Dautzenbergia*, the taxonomy of this genus is very disorganized (Diviacco 1983), and the original description of *D. megacheir* from specimens collected in the deep Irish Sea (Walker 1898) showed some morphological differences with the Mediterranean specimens that should be revised. The most evident is that Walker (1898) described (as *Sympleustes megacheir*) the species as “eyes wanting”, an aspect also reported by Chevreux (1935), after re-examination of the same specimens. Telson and Gn2 of Walker’s *S. megacheir* were also different than those of our specimens and the specimens by Diviacco (1983). In addition, specimens collected by Stephensen (1944) off of southeastern Greenland also differed in Gn2 morphology from those collected by Walker.

All *Dautzenbergia* species have had modified pereopod dactyls adapted to anchors in a substrate, such as corals (Myers and Hall-Spencer 2004), but the current information does not allow us to consider possible species-coral relationships as described for Pleustidae. Buhl-Mortensen and Mortensen (2004) did not find *Dautzenbergia* associated with deep-water gorgonians in the genera *Paragorgia* and *Primnoa* in the NE Atlantic, with amphipods collected

from colonies using a suction system mounted on the ROV. Finally, some Pleustidae are also found in the deep Mediterranean, cited as associated with gorgonians (Bellan-Santini et al. 1993). Since we did not find any Pleustidae attached to *I. elongata*, this group might be associated in the deep Mediterranean with other types of gorgonians, such as *Lophogorgia* spp., which are less abundant than Isidids and sporadically found in the deep Balearic Basin (Gili et al. 1987; own unpublished data). We found in our sampling another possible coral-associated amphipod, *Seba aloe*, although without establishing a strong link, as we found for *Dautzenbergia*, since we only found a small number of specimens (5) after washing the colonies. This is a rare species collected only once (1 specimen) by Cartes and Sorbe (1999) at a depth of 1263 m, which is a depth inhabited by sparse *Isidella* colonies. However, *S. aloe* was cited by Bellan-Santini et al. (1993) in a depth range (to 4009 m) that is clearly deeper than the *Isidella* distribution, and it is sometimes associated with wood pieces; therefore, perhaps this species could only use coral as a refuge. Amphipods have been observed in video images associated with corals (De Clippele et al. 2015) without logically establishing by their small size a complete determination (cited as probably Stegocephalidae or Stenothoidae) or collected with corals (Buhl-Mortensen and Mortensen 2004; Schwentner and Lörz 2020); in the last case, with Pleustidae exhibiting a strong relationship with cold corals, similar to what we found between *D. megacheir* and *I. elongata*. Pleustidae seems to specialize in such habitats (Myers and Hall-Spencer 2004; Schwentner and Lörz 2020); however, we did not find any of the Mediterranean species associated with isidids, including *Stenopleustes nodifer*, or associated with deep corals such as *Acanthogorgia*, *Paragorgia*, or *Paramuricea* (Schwentner and Lörz 2020). All this suggests that different families can follow a similar adaptative convergence to exploit habitats generated by different deep corals.

In addition to the natural patchy distribution of *I. elongata*, different human impacts, not only trawling but also other historical factors such as deforestation (as suggested by Pèrès 1985), can affect, e.g. removing coral fields from the bottom, increasing barriers for the dispersion of associated amphipods and enhancing the isolation of populations. We found *D. megacheir* in both mature and sparse fields of *Isidella* but not in areas with small, presumably recovering fields, suggesting that coral size is a more important factor than field coral density for amphipod habitats.

The rest of the epibionts collected on *Isidella* colonies did not have a strong dependence on corals. *Gibossaveruca* sp. is, after our cruise in 2020, a new genus/species in the Mediterranean fauna; however, its association with

corals is not species specific. The genus *Gibossaverruca* sp., similarly to all Verrucidae, occurred on a wide variety of substrates, e.g. on brachiopod shells and sea urchin spines, and, as occurred NW of Mallorca, on dead corals (Young 2002). Among the most strong associations found between crustaceans and corals (e.g. parasitic poecilostomatid copepods, Bulh Mortensen and Mortensen 2004), we also found some cirripeds (Pyrgomatinae) that are obligatory symbionts of scleractinian corals. This, however, is not the case for Verrucidae. We found a large number of specimens attached to dead colonies/remains, mainly close to the base of *Isidella* (in a part of the coral devoid of polyps), and at insular depths with lower OM content and near-bottom resuspension (low turbidity), which probably favour their strategy as filter feeders. The lower TOM found on the insular side of the basin, compared with mainland areas (compiled, e.g. in Cartes and Figueroa 2020), could restrict the distribution of Verrucidae associated with *Isidella* only around insular depths.

We observed in the northwestern Mallorca field the coincidence of two filter feeders (Verrucidae and the sea anemone *A. dorhni*), which seem to occupy different levels in the colony where they live attached, probably by utilizing different abilities to filter particles. Small sea anemones can be found attached to the stems of gorgonian corals (e.g. sea fans) but also on hydroids and worm tubes. *A. dorhni* was abundant and distributed on colony rami in the middle and high parts of colonies, which could be explained by exploiting the resuspended matter also exploited by *Isidella* polyps.

Finally, regarding the diversity of the entire macrofaunal community associated with *I. elongata*, the most mature fields (larger and with a higher density of colonies) had a clearly higher diversity of associated fauna. The size of colonies in the northwestern Mallorca field was clearly higher than that in other parts of the Mediterranean (Carbonara et al. 2020). There, cirripeds and the solitary coral *D. dianthus* were collected only associated with this mature community. In the case of the Caryophyllidae, this is consistent with the long lifespan of the solitary corals (up to 200 years, Risk et al. 2002; Adkins et al. 2004), although live and dead Caryophyllidae have been collected in the Balearic Basin associated with a variety of substrates, including some of anthropogenic origin such as amphorae pieces (authors, unpublished data). In contrast, the amphipod *D. megacheir*, the species most strongly associated with bamboo corals that may show dynamics of possible adaptative radiation, was found not only in mature fields but also in sparse fields and was only absent in areas with small colonies that apparently had regenerated after being impacted by trawling. The identification of such a strong association of species as those found for amphipods with cold corals suggests a possible way of speciation for

deep-sea fauna, regarding which existing knowledge is practically nil. In agreement with Schwentner and Lörz (2020), to observe and to know in greater detail these complex associations of the fauna associated with deep-water corals may provide more cogent arguments, if this is necessary, that can be utilized to protect these fragile ecosystems as a source of faunal diversity and diversification.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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