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**The role of gorgonians as engineering species, in the structure and diversity
of benthic communities**

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As the nominated University supervisor of this M.Sc. project by Guillem Corbera Pascual, I confirm that I have had the opportunity to comment on earlier drafts of the report prior to submission of the dissertation for consideration of the award of M.Sc. Oceanography.

Signed.....

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Table of contents

Abstract.....	4
1. Introduction	5
2. Materials and methods.....	8
2.1. Study area	8
2.2. Target species	10
2.3. ROV survey	11
2.4. Video analysis.....	11
2.5. Statistical analyses	12
3. Results	14
3.1. Relation between gorgonian density and the surrounding megafauna	15
3.2. Relation between gorgonian size and the surrounding megafauna	18
3.3. Relation between gorgonian attributes and megafaunal epibionts	20
4. Discussion.....	22
4.1. Effects of gorgonian density on megafauna	22
4.2. Effects of gorgonian size on megafauna.....	23
4.3. Effects of gorgonians on megafaunal epibionts	23
4.4. Evaluation of the different diversity indices.....	24
4.5. Comparing Weddell and Mediterranean Seas	25
4.6. Gorgonians as key organisms for diversity conservation and ecosystem restoration	25
4.7. Future research	26
Acknowledgements	27
References	27
Appendices	32

Abstract

Gorgonians are autogenic ecosystem engineers that create three-dimensional structures via their own tissues. Dense aggregations of these species are known to produce changes in the environment, modifying abiotic and biotic factors. A large number of species benefit from the positive effects caused by gorgonians, which can attract organisms from nearby habitats finally increasing the biological diversity of the habitat. Despite their ecological importance in the functioning of ecosystems, this is the first attempt to analyse the effects of gorgonian population traits, such as density and size, on the surrounding megafaunal organisms and epibionts, using video-transects as reference material. The images used for this project were recorded by means of ROVs in two very contrasting environments: the Mediterranean and the Weddell Sea. Images covered an area of 420 m² where over 7000 organisms could be identified. Statistical analyses showed that increases in gorgonian density and size have a positive effect on megafaunal species richness and diversity, although the strength of such relationships was not equivalent. Density seems to play a more important role in determining megafaunal diversity than population structure does. In the case of epibionts, both gorgonian attributes were positively correlated to abundance and species richness. These results are probably explained by the changes that highly dense patches of gorgonians produce to the environment surrounding, mainly to water currents and sediment transport, as well as the opportunity that these aggregations offer to the associated fauna to find places to settle and hide from predators.

1. Introduction

Gorgonians (Cnidaria: Anthozoa) are sessile organisms that display a three-dimensional structure similar to that of hard corals, generally acting as a framework for the establishment of a diverse range of benthic organisms (Buhl-Mortensen & Mortensen, 2005). Dense aggregations of marine benthic engineering species are known to be of utmost importance for the associated fauna in shallow seas, but they become even more so in the deep ocean, where a lack of hard substrate is a common feature (Buhl-Mortensen *et al.*, 2010; Gutiérrez *et al.*, 2011). However, although their ecological importance in the functioning of the ecosystem seems relevant, continental shelf and deep-sea gorgonian communities have not been as studied as their coastal counterparts

Regardless of the depth, these species tend to create dense meadows popularly known as coral gardens, understood as assemblages with high densities of non-reef-forming corals that promote both physical and biological changes to the surrounding habitat (Bullimore *et al.*, 2013). Relatively non-altered communities can be found on Antarctic waters, where dense populations have been recorded in the past few decades (e.g. Gutt & Starman, 1998; Orejas *et al.*, 2002). The same situation has also been observed in the Mediterranean Sea, where dense communities of gorgonians, white and black corals have been registered despite the elevated anthropogenic pressure exerted over them (Weinbauer & Velimirov, 1996; Bo *et al.*, 2011; Freiwald *et al.*, 2002; Bo *et al.*, 2013). In such communities, engineering species biophysically affect either directly or indirectly the availability resources (e.g. food, space and shelter) and therefore affect the diversity of the area at a local scale (Jones *et al.*, 1997).

Owed to these characteristics, gorgonians can be considered autogenic ecosystem engineers, in the sense that they change the environment in which they live via their own physical structure (Jones *et al.*, 1994, 1997). Despite the importance of these organisms, there is a surprising lack of knowledge regarding the effects of gorgonians on the diversity of benthic communities. Only a few studies consider this subject, mainly focusing on meio- and macrofauna species (Buhl-Mortensen & Mortensen, 2005; Cerrano *et al.*, 2010; Curdia *et al.*, 2015). But there are almost no studies that relate the characteristics of gorgonians and their 3D dimensionality to megafaunal diversity (Buhl-Mortensen & Mortensen, 2005; Curdia *et al.*, 2015).

The main modification caused by gorgonians is the creation of a generally flexible structure that increases habitat complexity (Santavy *et al.*, 2013). Populations of gorgonians are typically composed of individuals of different heights depending on their age, ranging from a few centimetres to more than a meter (Buhl-Mortensen *et al.*, 2010). The presence of different sized individuals creates spaces in which bottom currents flow at different speeds, favouring the presence of microhabitats characterised by different environmental conditions (Buhl-Mortensen *et al.*, 2010). Since gorgonians are often located in regions with relatively high current speeds, dense aggregations produce differences in flow velocities. Highest current speeds occur at the limit of the population and at the top of the tallest individuals, which reach the fast laminar flow in the benthic boundary layer (Buhl-Mortensen *et al.*, 2010). In contrast, current speeds

are considerably reduced between colonies owed to the turbulent flow caused by the presence of the gorgonians' 3D structure. These lower current speeds promote higher sedimentation rates (Cerrano *et al.*, 2010), influencing the quantity and quality of the sediment, often deposited in the sheltered parts of the colonies and in between them (Buhl-Mortensen *et al.*, 2010; Gutiérrez *et al.*, 2011).

Besides the changes in current flow and sedimentation rates associated to gorgonian populations, these organisms also release mucus that traps organic particles in suspension and rapidly form aggregates that eventually sink to the seabed (Patton, 1972; Wild *et al.*, 2004). Mucus is released in large quantities when there is too much sedimentation and it contains higher carbon and nitrogen concentrations than other food sources (Marshall, 1968; Meikle *et al.*, 1988), contributing as an important source to the particulate organic matter composition in the benthic ecosystem. Furthermore, this mucus also participates in nutrient cycling through the so-called particle trapping (Mayer & Wild, 2010).

Animals that live in these coral gardens are protected from the strong currents by the structure of the gorgonians and also experience higher food availability thanks to the increased sedimentation rate and the mucus production (Connell, 1978; Meikle *et al.*, 1988; Wild *et al.*, 2004; Gutiérrez *et al.*, 2011). Deposit and suspension-feeders are the main beneficiaries of the high organic matter concentration present in the mucus secretions (Stachowicz & Hay, 1999), as well as the organisms living in the sediment interstices (e.g. nematodes), which also profit from this food source (Cerrano *et al.*, 2010).

The increase in structural complexity has also a positive effect on a vast range of other organisms, which seek shelter from predators between these biogenic structures (Buhl-Mortensen *et al.*, 2010; Gutiérrez *et al.*, 2011). Several fish species are known to spend part of their life cycle within gorgonian communities, especially during reproductive and larval stages, using them as spawning and nursery grounds (Gratwicke & Speight, 2005; Buhl-Mortensen *et al.*, 2010). This situation attracts, in turn, a large set of predators which significantly increase the number of trophic interactions (Gratwicke & Speight, 2005).

The complex structure of gorgonians also creates new habitable spaces between branches, internal spaces and crevices. These spaces are therefore available for colonisation by other organisms, such as crustaceans, polychaetes and echinoderms (Gutt & Schickan, 1998; Buhl-Mortensen *et al.*, 2010; Carvalho *et al.*, 2014). Most organisms that settle on gorgonians have commensal relationships with them, some of which have evolved to be obligate associates to certain species (Buhl-Mortensen *et al.*, 2010), and some can even be harmful to their host (e.g. *Alcyonium coralloides*) (Bo *et al.*, 2011). In the deep sea, the main epibionts found on top of gorgonians are crinoids, ophiuroids and holothurians (Gutt & Schickan, 1998; Goh *et al.*, 1999). These organisms seek suitable substrates to attach to, positioning themselves towards the fast laminar flow of the benthic boundary layer (Emson & Woodley, 1987; Fujita & Ohta, 1988). This flow carries higher loads of resuspended organic particles compared to the near bottom turbulent currents found at the base of gorgonian assemblages (Buhl-Mortensen & Mortensen, 2004; Buhl-Mortensen *et al.*, 2010).

The physical and biological effects caused by gorgonians are known to benefit many megafaunal species, attracting other organisms from nearby habitats, and thus increasing the diversity of the community. Jones *et al.* (1994) postulated that the effects of habitat modification depend on the density and the activity of the engineering organism. Therefore, it would be expected that the biophysical effects of gorgonians would be positively related to their density, which in turn would become a good indicator of the habitat species diversity. However, species richness and diversity do not depend exclusively on gorgonian density. Their morphology (unbranched, branched, planar, bushy, etc.) can also play an important role in determining the way in which species diversity increases with gorgonian density. Complex morphologies are probably better at providing refuge from predators and settlement space for epibionts (Santavy *et al.*, 2013). Overall, the expected general impact of the structure created by ecosystem engineers is an increase in diversity of the surrounding fauna that lives in the community (Jones *et al.*, 1994; Jones *et al.*, 1997).

Most of the research conducted in this subject in marine habitats is theoretical (Jones *et al.*, 1994, 1997; Hastings *et al.*, 2007; Gutiérrez *et al.*, 2011) and it is mainly based on hard corals and not gorgonians (Gratwicke & Speight, 2005; Idjadi & Edmunds, 2006). There are limited numbers of studies that relate the population structure of different gorgonians to an increase in benthic diversity (Cerrano *et al.*, 2010) and even less studies quantify how population and colony attributes may affect the characteristics of the community (Buhl-Mortensen & Mortensen, 2005; Curdia *et al.*, 2015).

Within the studies related to gorgonians, Cerrano *et al.* (2010) determined that sediments below gorgonian forests have higher nematode species richness than the ones in the surrounding non-engineered habitats. Buhl-Mortensen & Mortensen (2005) observed that species richness and abundance of gorgonian epibionts is correlated with the number of branches per colony, wet weight and percentage of exposed skeleton. A similar study was conducted by Curdia *et al.* (2015), in which colony attributes were related to different parameters of the associated epifaunal invertebrates, concluding that gorgonian size can be considered a driving factor in enhancing the abundance and richness of macrofaunal species in a region.

With regards to the way species diversity is calculated in this type of studies, a debate should be opened to decide which is the most appropriate index to be used (Jost *et al.*, 2010). Most studies of ecosystem engineering organisms use the Shannon-Wiener or the Gini-Simpson index as valid indices to calculate species diversity (Buhl-Mortensen & Mortensen, 2005; Cerrano *et al.*, 2010). Unlike species richness, they consider the number of species present in an area and the relative abundance of each of them (Gray, 2000). However, for some decades, several authors have claimed that the use of these indices embraces some methodological problems (Magurran, 1988; Gray, 2000; Jost *et al.*, 2010). The fact that these indices are nonlinear implies that each new taxon added to the assemblage has a smaller effect on the value of diversity obtained, even if all the taxa are equally abundant. This approach means that regardless of how many equally abundant taxa are added to a system, diversity values will eventually stop changing (Jost *et al.*, 2010). Therefore, these indices may be less consistent and trustworthy than

other alternatives (Gray, 2000; Jost *et al.*, 2010). MacArthur (1972) and Hill (1973) converted both indices to linear metrics, taking Shannon-Wiener index to its exponential (i.e. $\exp(H')$) and Gini-Simpson to its inverse (i.e. $1/1-H_{GS}$). As there are very little studies that address the problems associated with these two key indices (Gray, 2000), the present work will evaluate the results obtained using both the original indices and their modifications.

In summary, the present study aims to understand the way in which gorgonian assemblages affect the diversity of the surrounding megafauna using two benthic assemblages dwelling on very contrasting continental shelves as experimental setting. Conventional techniques, such as SCUBA diving, are not useful to obtain large data sets in shelf depths. For this reason, ROVs were used to access those populations and obtain quantitative data. ROVs are becoming more and more popular to investigate different parameters of the ecology of the deep-sea (Ondréas *et al.*, 2005; Robison *et al.*, 2010; Neves *et al.*, 2014), mainly because it allows reaching deep parts of the oceans at a relatively low cost. ROVs have become a very powerful tool to develop projects over large areas of the shelf and slope of most seas, allowing researchers to explore different biological assemblages without causing any damage to the benthic populations.

Based on the ideas brought up by Jones *et al.* (1994, 1997) and Curdia *et al.* (2015), this study expects to find an increase in the diversity and abundance of the surrounding fauna with increasing densities and sizes of gorgonian populations. Furthermore, larger and older gorgonians are expected to hold a greater number of epibionts. To answer these questions, our study has the following objectives:

Analyse two video-transects from Antarctica and two from the Mediterranean Sea dominated by different gorgonian species (*Thouarella variabilis* and *Eunicella cavolinii*) to determine if the abundance, species richness and diversity of megafaunal species are driven by the gorgonian population's structure.

Determine if the abundance and species richness of gorgonian epibionts is related to gorgonian density and size in both study areas.

Evaluate how diversity indices perform in these types of studies

2. Materials and methods

2.1. Study area

The surveys performed for the present study were conducted over the continental shelves of two very contrasting regions: Cap de Creus (northwestern Mediterranean Sea) (Fig. 1a) and the eastern Weddell Sea (Antarctica) (Fig. 1b).

Cap de Creus is located in the southernmost part of the Gulf of Lions. It consists of a relatively small cape, characterized by abrupt cliffs and small gravel beaches. The coast of the cape rapidly reaches the continental shelf, which is incised by a submarine canyon located less than 2 miles from shore in its nearest location. Continental shelf waters in the Gulf of Lions receive important fresh water and sediment inputs from the Rhone River, and move southward due to

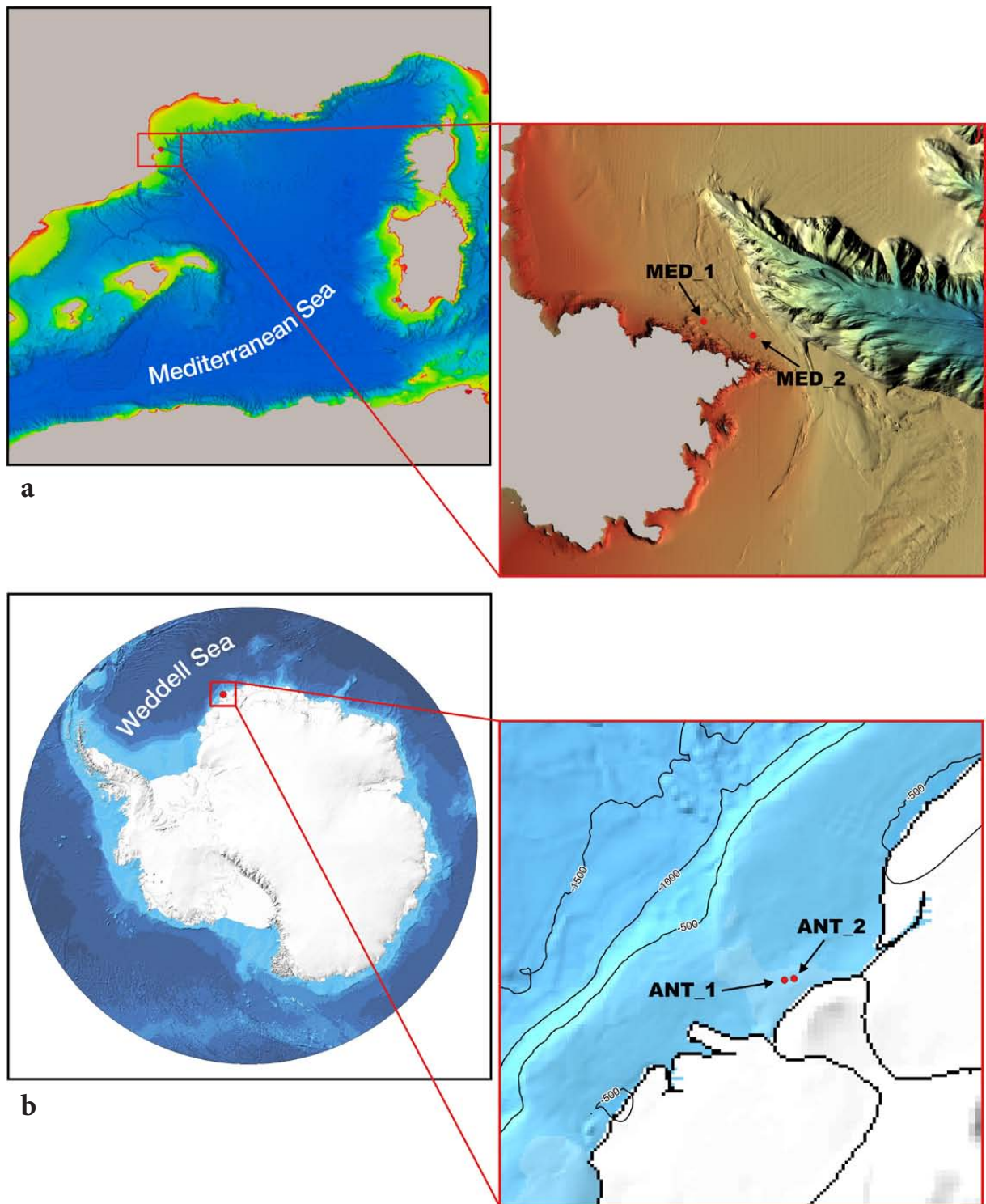


Figure 1. Location of all four ROV transects analysed for this study in the Mediterranean Sea (a) and Weddell Sea (b).

the dominant current system (Arnau *et al.*, 2004; Palanques *et al.*, 2006). The cold northern winds that characterize the winter period are responsible for the formation of dense water masses that sink through the submarine canyon of Cap de Creus, (Millot, 1999; Palanques *et al.*, 2006), transporting large quantities of sediment and organic matter through the shelf towards deeper regions (Got & Stanley, 1974; Palanques *et al.*, 2006; Ulses *et al.*, 2008). The effects of such phenomena may explain the high productivity of such region in terms of primary and secondary production (Crusado and Velasquez, 1990; de Bovée *et al.*, 1990).

The Weddell Sea is a region of the Southern Ocean, located between the Antarctic Peninsula and Cape Norvegia. In this area, an ice shelf permanently covers a major part of the southern region of the sea. Thus, almost all the regions close to the coast receive a significant amount of freshwater from the nearby ice sheets (Beckmann *et al.*, 1999). Similarly to the Gulf of Lions, the Weddell Sea has a crescent-shape continental shelf that gets narrower at the boundaries. At the easternmost boundary, east of Cape Norvegia, the maximum depth of the continental shelf is 400-500 m. However, the studied region has an overall depth range of 180-220 m.

2.2. Target species

Both study areas are characterized by the presence of different gorgonian species as the dominant ecosystem engineers (Fig. 2). The continental shelf of Cap de Creus holds dense patches of the octocoral *Eunicella cavolinii* (von Koch, 1887) (Fig. 2a), which dwells in sub-outcropping and outcropping rocky areas located in depths of 80-100 m between the cape and the nearby submarine canyon (Domínguez-Carrió *et al.*, 2014). *E. cavolinii* colonies are orange in colour and characterized by their two-dimensional fan-shaped structure (von Koch, 1887). Like other gorgonian species, *E. cavolinii* has been observed to orientate perpendicularly to prevailing water currents to maximise the efficiency of capturing food particles (Velimirov, 1973; Russo, 1985), distributing evenly in space to avoid overlapping one with each other (Russo, 1985). There are few studies regarding the population structure of this gorgonian species, but densities of over 18 colonies per m² have been observed on the west coast of Corsica (Velimirov & Weinbauer, 1992). Within *E. cavolinii* assemblages, it is usual to observe high percentages of colonies amassing a size of 10 cm or less, sometimes with this size-class representing in excess of 50% of the total population (Velimirov & Weinbauer, 1992).

On the other hand, one of the most abundant gorgonian species on the continental shelf east of Cape Norvegia (Weddell Sea, Antarctica) is *Thouarella variabilis* (Wright & Studer,



Figure 2. Target gorgonian species, *Eunicella cavolinii* from the Mediterranean Sea (a) and *Thouarella variabilis* from the Weddell Sea (b).

1889) (Fig. 2b), with densities of around than 50 colonies per 100 m² (Gutt & Starman, 1998). Colonies from this species are also orange in colour, but in contrast to *E. cavolinii*, they are formed by a unique axis often with very few ramifications (Zapata-Guardiola, pers. comm.). Small verticillated branches that bear polyps arise from the main axis and ramifications, giving *T. variabilis* a brush-like morphology. Regarding the average size of this gorgonian species, no previous works have been found. Therefore, the size measures obtained in the present study have been used to determine the size range of *T. variabilis* in the study area.

2.3. ROV survey

Seafloor images used in this study were recorded during two different expeditions. The Mediterranean survey was conducted on board the RV “Garcia del Cid” in September 2012. All images were recorded using Nemo ROV, a purpose built High Definition underwater filming robot equipped with a HD video camera (Sony 1080p). The Antarctic survey was carried out in the Weddell Sea, on board the RV “Polarstern” in April 2011. Images were recorded by means of the ROV Sperre SubFighter 7500 DC.

Although both surveys included a wide set of ROV dives in various locations, a selection of two ROV transects from each geographical region was chosen to carry out this study. Since the distance of every ROV dive varies widely, a fixed distance of 350 m was selected for each analysed transect, accounting for a total distance of 1400 m. The width of the analysed area was chosen to be 30 cm, providing total sampling area of 105 m² in each transect, which adds up to 420 m² overall.

The location of each transect was estimated by means of an USBL transponder mounted on the ROVs, which gave accurate GIS positions every 3 to 10 seconds. After projecting the ROV coordinates using the geographic data management software Quantum GIS 2.2.0, all points that had a extremely long distance from the previous position were eliminated, leaving a smooth geo-referenced transect.

Distances were calculated and 350 m long portions of each transect were selected. Both ROVs were equipped with parallel laser beams that projected two laser points over the seafloor at a fixed width. These points were used as reference to estimate the area to be analysed, as well as a reference to measure gorgonian height.

Finally, all transects were divided into five sections that approximately accounted for 7 minutes of video recording. In each section, ROV speed was calculated from the travelled distance. Such velocities were then used to calculate the position of each observed organism along the ROV transect. A summary of the main characteristics of each transect is given in Table 1.

2.4. Video analysis

Video images were analysed using the editing software Final Cut Pro 7.0.3 (Apple Inc). All transects were edited in order to remove those parts where the ROV was kept stationary (i.e.

Table 1. Geographical coordinates, depth and length for each of the analysed transects.

Transect	Coordinates		Depth (m)		Length (m)
	Start	End	Min.	Max.	
MED1	42°20'10"N, 3°19'44"E	42°20'8"N, 3°19'32"E	95	97	350
MED2	42°21'36"N, 3°16'36"E	42°21'25"N, 3°16'37"E	96	101	350
ANT1	70°54'35"S, 10°19'18"W	70°54'44"S, 10°19'19"W	209.8	212.3	350
ANT2	70°54'37"S, 10°22'21"W	70°54'36"S, 10°16'31"W	185.6	192	350

collection of samples or recording close-up images). Bad visibility sequences due to sediment resuspension or because the ROV was too far away from the seabed were also removed from the analysis. After removing the poor quality footage, good visibility sequences used in statistical analyses comprised a total length of 1315 m.

All visible megafaunal organisms that appeared along each transect within a section of 30 cm across the seabed were counted and identified to the lowest taxonomic level possible. Several organisms were impossible to identify to species level, so they were classified in higher taxonomic levels or even as morphospecies (e.g. white encrusting sponge). All epibionts, considered as organisms living on the top of the gorgonians, were also identified and noted down. Substrate type was visually determined, following two simple categories: rocky bottoms and soft substrates.

Density and abundance of gorgonians and the surrounding megafauna was then calculated dividing each transect in a set of 1.5 m² sampling units (5 m long fragments). Only those sampling units that contained at least one organism were considered. Overall, 263 sampling units were used in the following analyses, 138 corresponding to the Mediterranean Sea and 125 to the Weddell Sea.

The size of each gorgonian that appeared in all sampling units was measured by means of still pictures, taken when the parallel laser beams crossed the gorgonian base. Stills were processed using the image software Macnification 1.8 (Orbicule, Inc.), which allows measurements of the colonies by drawing a line from the base to the tip of the gorgonian following its principal axis.

2.5. Statistical analyses

A matrix containing the density data from all organisms excluding target species was created, for each transect, and analysed using the statistical software R 3.2.1 (R core team, 2015). To calculate the diversity of each sampling unit, the package *vegan* 2.2-1 (Oksanen *et al.*, 2015) was used. Several indices were used to calculate the diversity of these megafaunal organisms: Shannon-Wiener, exponential of Shannon, Gini-Simpson and inverse of Simpson.

Previous to all statistical analyses carried out, the density of each gorgonian species was plotted against the average size of the gorgonians in all sampling units to assess the independence of both variables. Pearson correlations and the Variance inflation factors were the tests used to know if there was a correlation between these two variables.

Gorgonian density and the average size of gorgonians in each sampling unit were plotted against the abundance of the rest of species, species richness and the 4 diversity indices calculated. The same was done for the abundance and species richness of gorgonian epibionts. All these data were compiled into one matrix (Appendices 1 & 2).

Spearman rank correlations were undertaken for gorgonian density versus species abundance, richness and diversity (i.e. Shannon-Wiener, exponential of Shannon, Gini-Simpson and inverse of Simpson). As this is a non-parametric test, data had no need to follow a normal distribution and thus values did not have to be transformed. For this analysis, p-values were calculated using the algorithm AS89, present in the basic R 3.2.1 software. The most statistically significant results were plotted showing gorgonian density and megafaunal diversity along the transect distance (x axis). Below the X axis a line indicating the type of substrate was added, in order to see if the relation between gorgonians and diversity could be affected by this factor. Spearman coefficient (ρ) values, which gives the degree of association between two variables and says whether this relationship is positive or negative, were added to each plot. Afterwards, linear regressions were then carried out give more details about these relationships.

Linear regressions were undertaken using the Ordinary Least Squares (OLS) method. In these regressions, the independent variables were density and size of the studied gorgonians, and the dependent variables were megafaunal abundance, species richness, diversity (i.e. one regression per diversity index), epibiont abundance and epibiont species richness. In total, eight linear regressions per transect were conducted.

Gorgonian density was log-transformed prior to all analyses because the data did not follow a normal distribution, as happened in some cases with megafaunal abundance. When doing the regressions between gorgonian size and all the dependent variables as well as the ones with epibiont data, the sampling units with no gorgonians were not considered. The regression lines were plotted only in the graphs where they are significant (p-value <0.05).

In order to be totally sure that gorgonian density and size were independent, the variable size was fixed (i.e. 5-10 cm) and an additional regression between gorgonian density and exponential of Shannon index was undertaken for the entire Mediterranean region. This analysis was only conducted for the specified region, because the Antarctic one did not have enough sampling units in a single size range to undertake it.

Finally, to assess the effect that different diversity may have had on the results, two analyses of variance (ANOVA) were undertaken. Diversities calculated using different indices could have distinctive effects in how they fit the regression models. Therefore, for both analyses, the data used were the coefficients of determination (R^2) from the linear regressions, which shows how good the data fits the regression model. For the first ANOVA, the coefficients of determination used were the ones obtained in the regressions between gorgonian density and the dependent variables. In contrast for the second one the coefficients used were the observed between gorgonian size megafaunal variables.

3. Results

From the 138 sampling units analysed in the Mediterranean Sea, 3366 individuals have been identified, belonging to 92 species and 9 phyla. The gorgonian *Eunicella cavolinii* and the sea pen *Pteroeides spinosum* were the most abundant species, accounting for 33% and 6% of the total abundance respectively. On the other hand, from the 125 sampling units analysed in the Weddell Sea region, 4076 individuals were identified, belonging to 94 different taxa and 11 phyla. The most abundant species was the bryozoan *Melicerita obliqua* followed by the gorgonian *Thouarella variabilis*, accounting for 30% and 12% of the total abundance, respectively.

Some organisms, mainly sponges and bryozoans, could not be identified to species or genus level and thus had to be classified into broader taxonomic groups or morfospecies. In the case of the Mediterranean transects, 65% of organisms were identified down to species or genus level, while 6% were included in broader taxonomic groups and 29% were identified as morfospecies. On the other hand, 41% of the organisms observed in the Antarctic transects were identified to species or genus level, while 13% were included in higher taxonomic groups and 46% were classified as morfospecies.

Regarding the target gorgonian species, *E. cavolinii* had an average density of 5.34 colonies/m² over the two analysed transects in the Mediterranean region. Density values oscillated between 0 and 27 colonies/m² in one transect and between 0 and 12 colonies/m² in the other. *T. variabilis* had a lower average density than its Mediterranean counterpart, with a value of 2.57 colonies/m² over the two Antarctic transects. Densities of this gorgonian ranged from 0 to 10 colonies/m² in one transect and 0 to 19 colonies/m² in the other.

A total of 1174 colonies of *E. cavolinii* were measured in the Mediterranean transects, while 361 *T. variabilis* in the Weddell Sea. *E. cavolinii* colonies had an average size of 7.04 cm. The tallest colony measured 30.15 cm, while in some areas, colonies were observed to be as small as 0.57 cm. From all these colonies, around 10% had epibionts living on top of them (10.83% and 9.05% in each transect respectively). The most common epibiont organism found on top of *E. cavolinii* was an unidentified species of Bryozoa. Colonies of *T. variabilis* had an average size of 21.08 cm, with some organisms as tall as 45.53 cm. The smallest colony recorded had a size of 7.28 cm. From all the colonies examined, 6.57% and 39.23% had epibionts living on top of them in each transect, respectively. The species *Staurocucumis* sp. was the most abundant organism living on top of *T. variabilis*.

Some of the most relevant environmental factors examined showed very constant values along the transects. Both continental shelves in the study areas were absolutely flat, with depth being almost invariable along each transect. Substrate type was homogeneous in both Antarctic transects and one Mediterranean, basically composed by medium sands and gravels all along. In contrast, the remaining transect from the Mediterranean Sea had parts composed by coarse gravels and pebbles (56%) and others with sub-outcropping and outcropping rocks (44 %).

Finally, collinearity was not observed between the independent variables (i.e. density and size), with values for Pearson correlation and Variance Inflation Factor below the threshold ($r < 0.7$) ($VIF > 0.1$).

Table 2. Results of the Spearman rank correlations between gorgonian density and the four analysed variables, undertaken for each transect. Significant p-values shown in bold; n.s. $p>0.05$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Transect	Variable	p-value		ρ
MED_1	Abundance	0.036	*	0.219
	Species richness	5.99E-07	***	0.551
	Exp. Shannon	1.82E-07	***	0.571
	1/Simpson	5.51E-07	***	0.551
MED_2	Abundance	0.033	*	0.223
	Species richness	1.85E-05	***	0.475
	Exp. Shannon	7.04E-06	***	0.5
	1/Simpson	1.90E-05	***	0.478
ANT_1	Abundance	6.00E-04	***	0.376
	Species richness	2.00E-04	***	0.415
	Exp. Shannon	9.01E-05	***	0.43
	1/Simpson	3.00E-04	***	0.401
ANT_2	Abundance	0.127	n.s.	0.158
	Species richness	3.10E-05	***	0.517
	Exp. Shannon	3.33E-08	***	0.675
	1/Simpson	5.18E-07	***	0.608

3.1. Relation between gorgonian density and the surrounding megafauna

Gorgonian density seems to have a significant effect on the surrounding species richness as well as over all the diversity indices tested according to the results of the Spearman rank correlations (Table 2). The highest ρ values (Spearman correlation coefficient) were observed between gorgonian density and both Shannon-Wiener and the exponential of Shannon indices in all four transects (Fig. 3). In fact, these two diversity indices showed the same result for all p-values and ρ . Figure 3 shows the exponential of Shannon index instead of Shannon-Wiener because its variations were easier to assess due to its non-logarithmic nature. Gorgonian density changes in Mediterranean transects correlate to variations in megafaunal diversity, almost with the same pattern ($\rho=0.571$ and $\rho=0.5$) (Fig. 3a,b). Similar results are observed in the Antarctic transect 2, in which the ρ value for gorgonian density and exponential of Shannon index is 0.675 (Fig. 3d). On the other hand, in the Antarctic transect 1 gorgonian density falls after some oscillations (Fig. 3c). Regardless of this particular situation, values for all megafaunal diversity indices oscillate almost around the same values to those observed in areas where *T. variabilis* density is high. Therefore, the correlation coefficient value decreases to a lower value compared to the other 3 transects ($\rho=0.430$).

In the case of the linear regressions, the formula given by the regression line of each relation, shows how much dependent variables change due a change in gorgonian density (Table 3). Results of this parametric analysis showed that gorgonian density positively correlated with megafaunal abundance in two of the four transects, one from each region (Table 3). Although these two regressions showed p-values lower than 0.01, there was still a lot of dispersion ob-

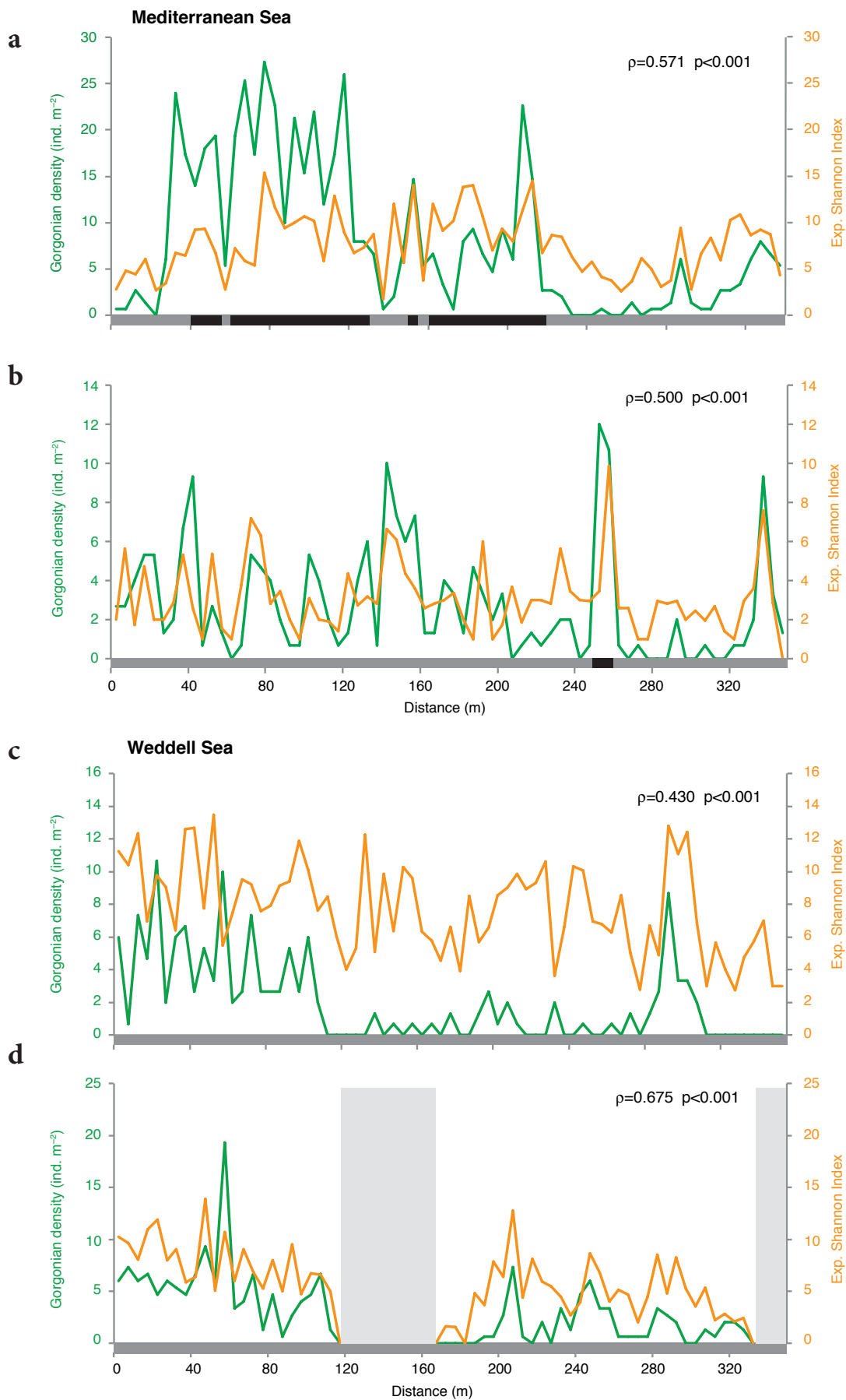


Figure 3. Changes in the exponential of Shannon index (yellow) with changes in gorgonian density (green) along Mediterranean (a, b) and Weddell Sea (c, d) transects. Substrate type is shown as a colour band at the bottom of each plot: soft substrates in grey and hard substrates in black.

Table 3. Results of the linear regressions between gorgonian density and the six analysed variables, undertaken for each transect. Significant p-values shown in bold; n.s. $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Transect	Variable	Formula	F	p-value		R ²
MED_1	Abundance	$y = 2.909x + 20.988$	3.081	0.084	n.s.	0.03
	Species richness	$y = 2.389x + 5.952$	27.21	1.98E-06	***	0.281
	Shannon	$y = 0.389x + 2.092$	31.57	4.18E-07	***	0.313
	Exp. Shannon	$y = 1.766x + 4.525$	29.42	8.89E-07	***	0.298
	Simpson	$y = 0.054x + 0.701$	26	3.09E-06	***	0.272
	1/Simpson	$y = 1.309x + 3.782$	25.56	3.64E-06	***	0.268
MED_2	Abundance	$y = 1.822x + 4.980$	7.868	6.50E-03	**	0.092
	Species richness	$y = 1.553x + 1.889$	27.87	1.51E-06	***	0.283
	Shannon	$y = 0.544x + 0.875$	22.7	1.08E-05	***	0.245
	Exp. Shannon	$y = 1.328x + 1.756$	28.55	1.22E-06	***	0.291
	Simpson	$y = 0.143x + 0.393$	14.83	2.68E-04	***	0.171
	1/Simpson	$y = 1.142x + 1.667$	26.82	2.84E-06	***	0.278
ANT_1	Abundance	$y = 0.362x + 2.843$	10.05	2.20E-03	**	0.115
	Species richness	$y = 2.116x + 9.253$	14.02	4.00E-04	***	0.157
	Shannon	$y = 0.322x + 2.6$	15.49	2.00E-04	***	0.172
	Exp. Shannon	$y = 1.56x + 6.556$	15.94	2.00E-04	***	0.176
	Simpson	$y = 0.04x + 0.771$	8.412	5.00E-03	**	0.096
	1/Simpson	$y = 1.146x + 5.155$	11.83	1.00E-03	**	0.134
ANT_2	Abundance	$y = 0.255x + 2.690$	3.37	0.072	n.s.	0.043
	Species richness	$y = 3.564x + 5$	27.2	3.22E-06	***	0.331
	Shannon	$y = 0.632x + 1.705$	33.9	3.67E-07	***	0.383
	Exp. Shannon	$y = 2.519x + 3.187$	37.55	1.21E-07	***	0.408
	Simpson	$y = 0.126x + 0.562$	21.67	2.27E-05	***	0.281
	1/Simpson	$y = 1.997x + 2.398$	24.56	8.04E-06	***	0.308

served. This is reflected in the low R² values of 0.092 and 0.115 in the Mediterranean and Antarctic transect respectively.

With regards of the species richness, it showed a significantly positive correlation with gorgonian density in all studied transects. The four linear regressions gave a p-value lower than 0.001 as a result (Table 3). In this case, less dispersion was observed, with the Mediterranean transects showing R² values of 0.281 and 0.283 (Fig. 4a). Similar correlation values were observed in Weddell Sea transects, which had R² values of 0.157 and 0.331 (Fig. 4b).

Linear regressions calculated using diversity indices as dependent variables, showed that diversity had a significantly positive correlation with gorgonian densities in all the cases (p-value < 0.001) (Table 3). Determination coefficients for the exponential of Shannon index were quite high, with an R² of 0.297 in the Mediterranean transect 1 and an R² of 0.408 in the Antarctic transect 2 (Fig 4c,d).

Lastly, the regression undertaken between gorgonian density and species richness, as well as with the exponential of Shannon index for a particular gorgonian size class (i.e. 5-10 cm) showed a significantly positive correlation between all variables (p-values lower than 0.001).

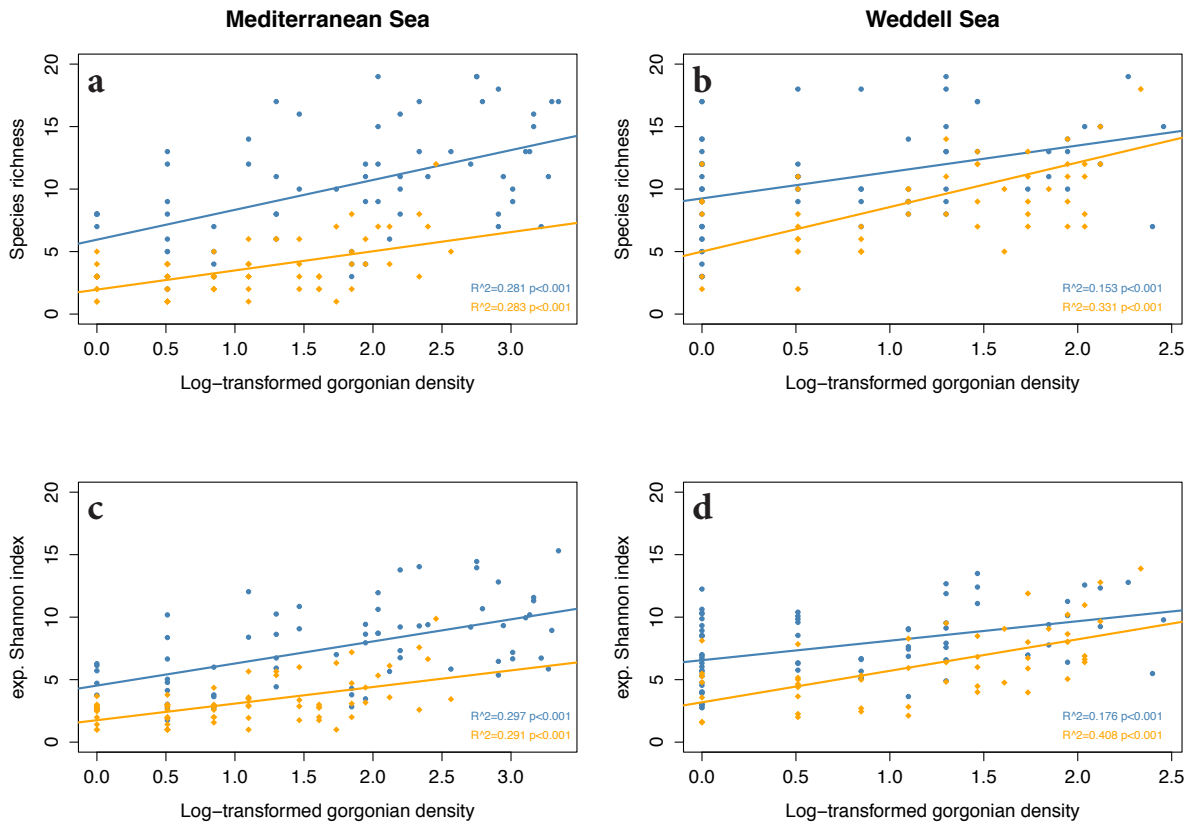


Figure 4. Linear regressions between gorgonian density and species richness of Mediterranean (a) and Weddell Sea transects (b). Below, linear regressions between gorgonian density and exponential of Shannon index of Mediterranean (c) and Wedell Sea transects (d). MED_1 and ANT_1 transects are represented in blue and MED_2 and ANT_2 transects in yellow.

The determination coefficients obtained were some of the highest observed in the present study ($R^2=0.468$, $R^2=0.417$).

With regards to the dispersion of the values in the regressions, the Shannon-Wiener index (H') and its modified version ($\exp H'$) do not show a significantly better performance than the Simpson indices in any transect, (ANOVA p-value >0.05). Although R^2 values obtained from the modified indices ($\exp H'$ and $1/\text{Simpson}$) were usually higher than the ones from original diversity indices (i.e. Shannon-Wiener and Gini-Simpson), no significant differences were observed between the determination coefficients (ANOVA p-value >0.05).

3.2. Relation between gorgonian size and the surrounding megafauna

Size significantly affected megafaunal abundance only in the Mediterranean transect 2 (p-value < 0.05) (Table 4). However, there was a lot of point dispersion around the regression line and the determination coefficient was very low ($R^2=0.065$). The same situation was observed when relating gorgonian size and species richness (Table 4). Species richness only positively correlated to gorgonian size in the Mediterranean transect 2 (p-value=0.01, $R^2=0.099$) (Fig. 5a). Antarctic transects showed no significant correlation between gorgonian size and species richness (Fig. 5b). However, if both transects were considered together, a significant positive correlation could be observed (p-value <0.01 , $R^2=0.104$).

Table 4. Results of the linear regressions between gorgonian size and six analysed variables, undertaken for each transect. Significant p-values shown in bold; n.s. $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Transect	Variable	Formula	F	p-value		R ²
MED_1	Abundance	$y = 0.129x + 25.149$	0.019	0.89	n.s.	-0.017
	Species richness	$y = 0.201x + 9.465$	0.49	0.487	n.s.	-0.009
	Shannon	$y = 0.017x + 2.754$	0.148	0.701	n.s.	-0.014
	Exp. Shannon	$y = 0.106x + 7.381$	0.27	0.606	n.s.	-0.012
	Simpson	$y = -6.16E-05x + 0.807$	9.40E-05	0.992	n.s.	-0.017
	1/Simpson	$y = 0.066x + 5.970$	0.17	0.68	n.s.	-0.014
MED_2	Abundance	$y = 0.317x + 4.386$	4.854	0.032	*	0.065
	Species richness	$y = 0.194x + 2.177$	7.03	0.01	*	0.099
	Shannon	$y = 0.077x + 0.927$	8.93	0.004	**	0.128
	Exp. Shannon	$y = 0.187x + 1.882$	9.33	0.004	**	0.133
	Simpson	$y = 0.021x + 0.406$	7.35	0.009	**	0.105
	1/Simpson	$y = 0.167x + 1.736$	9.76	0.003	**	0.14
ANT_1	Abundance	$y = 0.001x + 3.337$	0.009	0.926	n.s.	-0.025
	Species richness	$y = 0.114x + 9.476$	1.6	0.213	n.s.	0.015
	Shannon	$y = 0.028x + 2.375$	6.12	0.018	*	0.111
	Exp. Shannon	$y = 0.155x + 4.943$	5.81	0.021	*	0.105
	Simpson	$y = 0.005x + 0.701$	6.38	0.016	*	0.116
	1/Simpson	$y = 0.114x + 3.944$	3.59	0.065	n.s.	0.06
ANT_2	Abundance	$y = 0.005x + 2.899$	0.01	0.923	n.s.	-0.029
	Species richness	$y = 0.205x + 5.808$	0.636	0.431	n.s.	-0.011
	Shannon	$y = 0.056x + 1.509$	2.73	0.108	n.s.	0.047
	Exp. Shannon	$y = 0.205x + 2.583$	2.53	0.121	n.s.	0.042
	Simpson	$y = 0.012x + 0.512$	2.35	0.135	n.s.	0.037
	1/Simpson	$y = 0.175x + 1.711$	2.3	0.139	n.s.	0.036

With regards to megafaunal diversity, linear regressions were statistically significant only in two of the four transects analysed. One of them is the Mediterranean transect 2, in which all diversity indices were significantly correlated to gorgonian size (p-value < 0.01) (Table 4). However, the determination coefficients were low, being the exponential of Shannon index the regression with the highest value ($R^2 = 0.133$) (Fig. 5c). The other transect with statistically significant results was the Antarctic transect 1. Gorgonian size had a statistically significant correlation with three of the four diversity indices (Shannon-Wiener, exponential of Shannon and Gini-Simpson indices), with p-values lower than 0.05 (Table 4 and Fig. 5d). Despite their significance, a lot of dispersion could be observed. The highest value for the determination coefficient was $R^2 = 0.116$, which was in the relationship between gorgonian size and the Gini-Simpson index.

The performance of the different diversity indices did not show any trend in these analyses (ANOVA p-value < 0.05). The determination coefficients were very similar in all the statistically significant regressions, regardless of the diversity index used (Table 4).

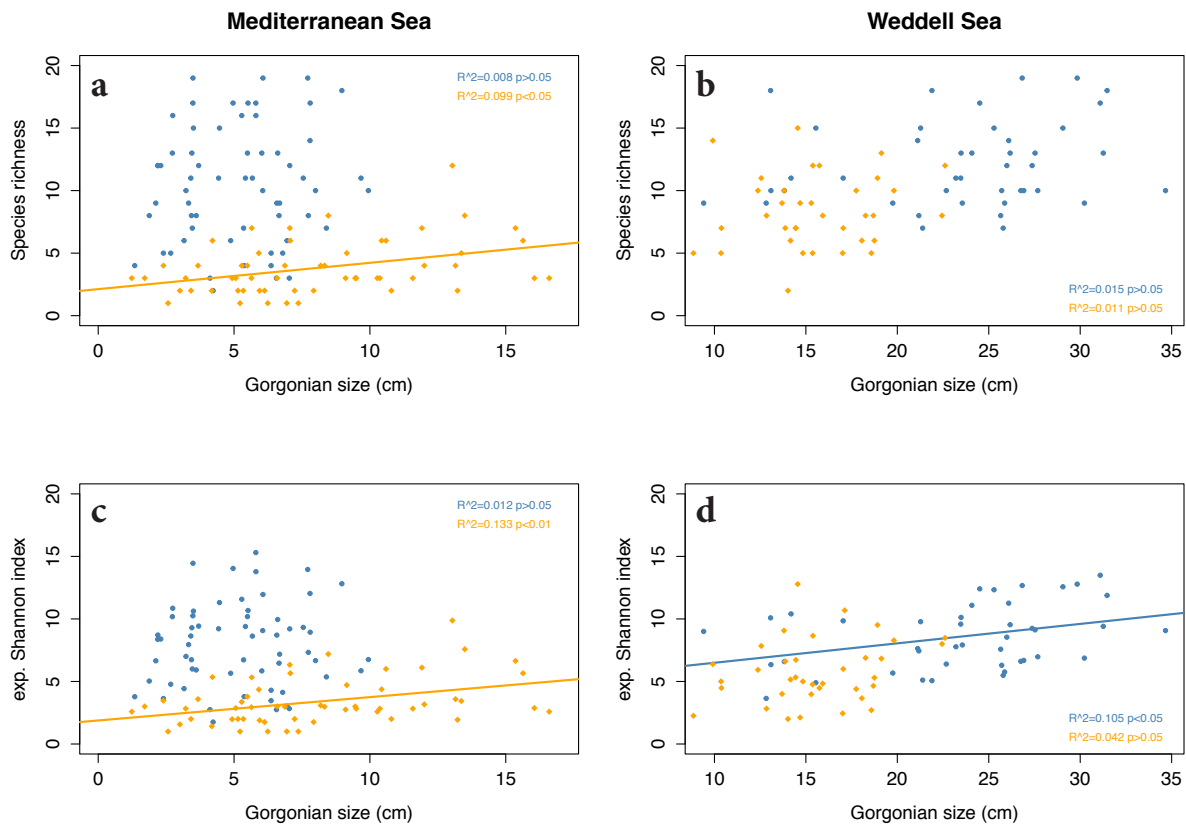


Figure 5. Linear regressions between gorgonian size and species richness of Mediterranean (a) and Weddell Sea transects (b). Below, linear regressions between gorgonian size and exponential of Shannon index of Mediterranean (c) and Wedell Sea transects (d). MED_1 and ANT_1 transects are represented in blue and MED_2 and ANT_2 transects in yellow.

3.3. Relation between gorgonian attributes and megafaunal epibionts

The linear regressions between gorgonian density and abundance of epibionts showed that these two variables positively correlate in all studied transects and that these relations were statistically significant (p-values <0.001) (Table 5). The determination coefficients for these regressions were the highest among all the analyses conducted in this study (Table 5). The Antarctic transect 1 showed an R² value of 0.592, meaning that the points from the analysis adjust quite well to the regression line created.

Regarding species richness, its relation to gorgonian density was significant in all analysed transects (p-values <0.001) (Table 5). In this case, the highest determination coefficient observed in the regression was in the Mediterranean transect 1 (R²=0.435).

Besides gorgonian density, regressions between size of the colonies and epibiont abundance were positive and statistically significant in all transects (p-values <0.01) (Table 5), but the Antarctic transect 2 (Fig. 6). In general the determination coefficients were lower than the case of gorgonian density. The highest R² value was found in the Mediterranean transect 1 (R²=0.211) (Fig. 6a).

Finally, all transects except Antarctic transect 2 showed a significant correlation between the species richness of the epibionts and gorgonian size (p-values <0.01) (Table 5). In this case, the highest determination coefficient was observed in the Mediterranean transect 2 (R²=0.225)(Fig. 6c).

Table 5. Results of the linear regressions of gorgonian density and size against epibiont abundance and epibiont species richness, undertaken for each transect. Significant p-values shown in bold; n.s. $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Transect	Factor	Variable	Formula	F	p-value	R ²
MED_1	Gorgonian density	Abundance	$y = 0.589x - 0.563$	86.82	3.39E-13 ***	0.589
		Species richness	$y = 0.874x - 0.802$	47.21	4.47E-09 ***	0.435
MED_2		Abundance	$y = 1.020x - 0.531$	31.64	3.93E-07 ***	0.311
		Species richness	$y = 0.718x - 0.341$	33.39	2.15E-07 ***	0.323
ANT_1		Abundance	$y = 1.215x - 0.493$	60.57	1.56E-09 ***	0.592
		Species richness	$y = 1.324x - 0.381$	27.36	5.66E-06 ***	0.391
ANT_2		Abundance	$y = 0.359x - 0.267$	15.53	3.00E-04 ***	0.24
		Species richness	$y = 0.406x - 0.291$	15.28	3.00E-04 ***	0.237
MED_1	Size	Abundance	$y = 0.158x - 0.242$	17.07	1.00E-04 ***	0.211
		Species richness	$y = 0.238x - 0.348$	12.4	8.00E-04 ***	0.16
MED_2		Abundance	$y = 0.171x - 0.729$	14.81	3.00E-04 ***	0.201
		Species richness	$y = 0.122x - 0.500$	16.99	1.00E-04 ***	0.225
ANT_1		Abundance	$y = 0.065x - 0.439$	8.4	6.00E-03 **	0.153
		Species richness	$y = 0.081x - 0.578$	7.4	9.00E-03 **	0.135
ANT_2		Abundance	$y = 0.011x + 0.01$	0.26	0.612 n.s.	-0.022
		Species richness	$y = 0.010x + 0.063$	0.16	0.692 n.s.	-0.025

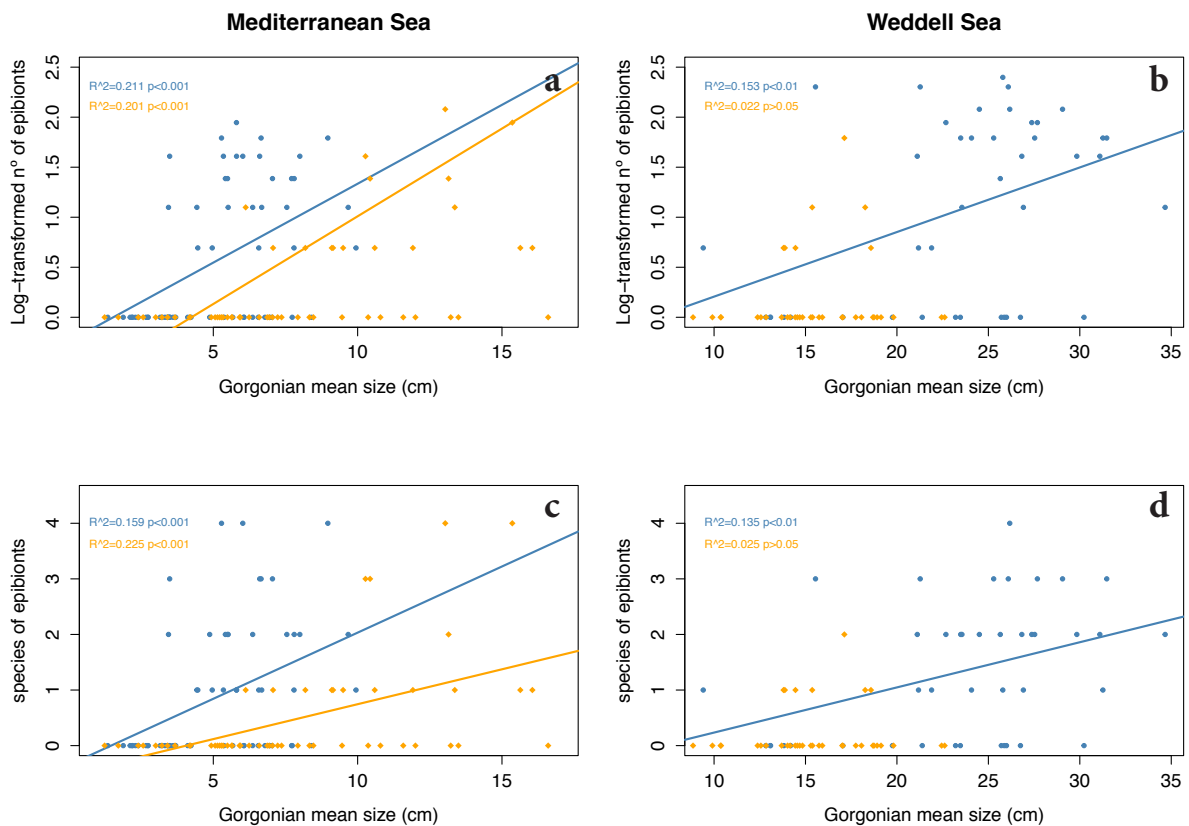


Figure 6. Linear regressions between gorgonian size and log-transformed abundance of epibionts of Mediterranean (a) and Weddell Sea transects (b). Below, linear regressions between gorgonian size and epibiont species richness of Mediterranean (c) and Weddell Sea transects (d). MED_1 and ANT_1 transects are represented in blue and MED_2 and ANT_2 transects in yellow.

4. Discussion

4.1. Effects of gorgonian density on megafauna

Contrary to what was originally expected, there was no clear relationship between gorgonian density and the abundance of megafaunal species, a trend was only observed in two of the four analysed transects (Table 3). In Mediterranean transect 1, the presence of three very abundant species (*Alcyonium palmatum*, *Epizoanthus* sp. and *Smittina cervicornis*) in areas with low gorgonian density are probably the cause for the non-significant regression results. The same happened in Antarctic transect 2, in which low gorgonian density areas were largely occupied by accumulations of the bryozoan species *Melicerita obliqua*. These results, however, do not incorporate the biomass of megafaunal species, since there is no possible way to estimate these types of values from the video images. Small organisms, in this way, may be overrepresented when using abundance as a proxy to evaluate the influence of gorgonian density in the surrounding megafauna.

On the other hand, the effects of gorgonian density on species richness and biodiversity give support to the hypothesis suggested at the beginning of the project. Gorgonian density positively correlates with species richness and diversity in both regions, Mediterranean and Weddell Sea. (Fig. 3 and 4). The two different statistical tests used gave similar results: (1) the Spearman correlations showed the coupling of these variables along the transects and (2) the linear regressions gave information about the strength of such relationships (i.e. how the values in axis Y change with changes in axis X).

Gorgonian species can be considered autogenic engineers that act as foundation species because of the changes that these organisms produce on the abiotic factors (e.g. lower current velocities and increases in sedimentation rates). These way gorgonians facilitate the colonisation of other species that otherwise would not be able to live there, also giving protection from predators to a vast range of organisms. Therefore, and according to Jones *et al.* (1997), it must be assumed that the higher the density of these organisms, the stronger the effects of such changes. This means that more colonies would result in higher stress amelioration and more places to hide from predators, which would increase species richness and diversity, as it has been observed in our study.

It is important to point out that gorgonian density is not the only factor that can benefit other taxa. Hard substrates, such as outcropping rocks or biogenic formations, are also known to enhance species diversity through an increase in the heterogeneity of the region (MacArthur & Wilson, 1967), for example supplying more spaces for larval settlement of other species. This fact could explain why the recorded values of diversity were kept high in some parts of Mediterranean Transect 1, even though gorgonian density fell. It seems, however, that in areas with hard substrates and high gorgonian densities, these two factors joined forces to further increase the diversity values. Moreover, it could be observed that diversity followed the effect of gorgonian density, with oscillations of both values in total synchrony, reaching higher peaks in

hard substrate regions when compared to soft substrates (Fig. 3). Diversity seems to be incapable of increasing after certain values of density are reached, as observed in the first part of the Mediterranean transect 1. This fact could explain the slightly higher dispersion observed in the regression plot for this transect in comparison to the Mediterranean transect 2.

On the other hand, in the Antarctic transect 2 there was a decoupling between gorgonian density and megafaunal diversity without any apparent changes in substrate. The fact that diversity kept oscillating at high values while density was very low could be explained by the presence of other organisms that may be structuring the community, such as *Stylocordyla chupachups*, which had considerably high densities in that part of the transect. This decoupling may be the reason to why R^2 values of most of the regressions in this transect were much lower compared to the other Antarctic transect.

4.2. Effects of gorgonian size on megafauna

As seen in Curdia *et al.* (2015), large gorgonians supposedly increase habitat complexity and thus species richness and diversity. Our study showed that this relationship was only significant in two of the analysed transects, with p-values less significant to those obtained by gorgonian density.

There may be a few reasons to explain why gorgonian size did not show a strong relationship with species richness and diversity. Firstly, in three of the transects, especially the two from the Weddell Sea, the size range observed was maybe too small to appreciate such relationship. All gorgonians in one of the Antarctic transect were small, while they were large in the other. However, if both transects were analysed together, a positive and significant relationship between gorgonian size and species richness, as well as diversity, could be observed. Other problems besides the small range of sizes could have affected the results in Mediterranean transect 1. Here, high diversities caused by the presence of hard substrate could have masked the effect of gorgonian size on the surrounding megafauna. Finally, although gorgonian size was observed to significantly affect species richness in the experiment performed by Curdia *et al.* (2015), the authors focused on macrofaunal species, not only on megafauna. Therefore, gorgonian size may be an important factor promoting species diversity, but probably at a different scale than the analysed in this project.

4.3. Effects of gorgonians on megafaunal epibionts

Gorgonian density showed a positive significant relationship with epibiont abundance and species richness, as it was expected at the beginning of the study. No other work has been found that relates these variables. An increase in epibiont abundance should be expected with increases in gorgonian density, since the higher the density, the higher available substrate. But our results suggest that the main effect regulating the presence and abundance of epibionts is the size of the gorgonian.

Some of the main megafaunal epibionts found in Antarctica in the present study (e.g. *Staurocucumis* sp. and *Promachocrinus* sp.) correspond to those observed by Gutt & Schickan (1998). These authors conclude that megafaunal epibionts mostly look for gorgonians to live on in order to reach a fast laminar water flow, which has more particles in suspension. Therefore, taller gorgonians should be a better substrate to settle on, in order to take profit of this type of food source.

For organisms living on top of gorgonians, several other articles describe how their number and diversity increase with colony size (Carvalho *et al.*, 2014, Curdia *et al.*, 2015). Although these works mainly focus on macrofauna, similar results could be expected for megafaunal epibionts in the present study. In our case, the effect of gorgonian size on abundance and species richness of epibionts was found significant in three of the four transects. However, the huge amount of gorgonians without any epibionts living on top of them, especially small colonies, probably cause a decrease in the R^2 values. The effects on epibiont abundance and species richness followed the same pattern in all 4 transects, with the exception of the Antarctic transect 2 that was not significant in any of the analyses. The later seems to suffer from the same problem that affected the significance of its megafaunal results, in which the size range for this transect was too small to show any significant relation.

Several processes could explain the positive relation between size and the abundance and species richness of epibionts. Large colonies have more space for epibiont settlement and therefore, they allow more organisms to live on top of them (Carvalho *et al.*, 2014). Furthermore, large gorgonians have also been present in the environment for longer than small ones, time during which they could have been colonised by several epibionts. Lastly, larger colonies tend to be older organisms, and their chemical defences may not be as efficient to defend themselves from the settlement of epibionts (Dube *et al.*, 2002).

It has to be pointed out that high abundances of epibionts have been observed living on top of small gorgonians in Mediterranean transect 1, which could related to the effects of long-line fishing, very common in the region. Long-lines are known to cause wounds on the gorgonian tissue, allowing other organisms to settle on (Bavestrello *et al.*, 1997; Cupido *et al.*, 2007).

4.4. Evaluation of the different diversity indices

Several works have assessed the use of biodiversity indices to calculate species diversity (e.g. Whittaker, 1972; Magurran, 1988; Gray, 2000; Jost *et al.*, 2010). In the present study, one of the objectives was to evaluate how the choice of a certain index can affect the results, in this case, the R^2 values obtained in the linear regressions. Gray (2000) exposed that the exponential of Shannon and 1/Simpson indices are more sensitive to changes in the number of species than Shannon-Wiener and Gini-Simpson. However, it should be considered that changes in the Shannon-Wiener index are logarithmic, which mean that small increases in the values obtained would reflect big changes in the ecosystem.

Our results suggest that both versions of Shannon-Wiener index achieved a better fit in almost all linear regressions (i.e. higher R^2 values). It was also observed that linear regressions obtained using the modified versions of Shannon-Wiener and Gini-Simpson indices had R^2 values considerably higher than the original indices. However, after performing an ANOVA test between all used indices, p-values showed that there were no significant differences between any of the R^2 values obtained.

The modified versions of the indices have a wider range of values than the original ones, which makes them more sensitive to changes in diversity. Therefore, although the results did not show any significant effect in the case of using one index or the other, the exponential of Shannon and 1/Simpson would probably be the best suited for this kind of analyses.

4.5. Comparing Weddell and Mediterranean Seas

The effects of gorgonian density and size observed in two totally contrasted regions, with similar depth ranges and two different gorgonian species (*E. cavolinii* and *T. variabilis*) were equivalent. Variations in the effects of gorgonian density and size on the studied fauna, however, did occur. This was the case of gorgonian density, in which Weddell Sea values had a slightly better fit to the regression model than the Mediterranean Sea (i.e. higher max R^2 values).

The Mediterranean Sea has suffered from a very strong human pressure since the beginning of civilisation, and it still holds an important artisanal fishery. Some of the methods most widely used are long-lines and trammel nets, which exert an effect on benthic organisms, especially gorgonians and corals due to their fragile structure (Fosså *et al.*, 2002; Althaus *et al.*, 2009; Sampaio *et al.*, 2012). Warwick & Clarke (1993) observed that increasing levels of disturbance can cause higher variability in species diversity. Therefore, such fishing methods and their frequent use in the Mediterranean shelf areas might explain the lower R^2 values observed in this area.

Finally, gorgonian density was observed to be more important than size at promoting higher diversities in both areas (i.e. more significant and with a better model fitting). This may mean that the amount of gorgonians dwelling in an area could affect diversity in a more profound way than their sizes, although it is very clear that areas with high densities and large sizes would empower even higher diversity values.

4.6. Gorgonians as key organisms for diversity conservation and ecosystem restoration

In most of the seas, gorgonians and other benthic fauna from the continental shelf are increasingly being affected by anthropogenic disturbances, such as bottom trawling and long-line fishing (De Groot, 1984; Bavestrello *et al.*, 1997; Reed *et al.*, 2005; Queirós *et al.*, 2006; Cupido *et al.*, 2007). The former fishing method is known to be very destructive and its impacts are only comparable to the massive forest clear-cutting (Watling & Norse, 1998), significantly

affecting benthic ecosystems. Gorgonians are almost completely depleted after trawling events and any survivors may die from collapse due to the huge amount of sediment that is resuspended (Cortés & Risk, 1985).

In this study, high gorgonian densities were associated to elevated species richness and diversities and, therefore, mass mortalities of these octocorals could have devastating effects on the local diversity (Coleman & Williams, 2002). Furthermore, the destruction of their structures could also affect the water-sediment processes (Coleman & Williams, 2002).

The critical role of structuring organisms, such as gorgonians, for the ecosystem has huge implications for conservation biology. Therefore, for all their positive ecosystem outcomes acknowledged in this project and other studies (Buhl-Mortensen *et al.*, 2010; Cerrano *et al.*, 2010; Gutiérrez *et al.*, 2011; Santavy *et al.*, 2013), there is a need to protect gorgonians from these highly frequent fishing activities and other anthropogenic disturbances. Although traditional conservation efforts have focused on the protection of charismatic taxa (Crain & Bertness, 2006), the findings of the present study enhance the idea of protecting the species that are more critical for the ecosystem functioning. Gorgonians, like any other ecosystem engineers, would be particularly useful as keystone species in conservation plans, because managing a single species could have a huge effect in the entire community (Crain & Bertness, 2006).

Results from the present study also show that gorgonians are capable of increasing diversity even at very small local scales (Fig. 3). This fact could help towards the design of management plans in marine protected areas, since small extensions dominated by gorgonian species could be exerting an important effect on the diversity of the region.

Besides the need for conservation, gorgonians are ecosystem engineers that act as foundation species (Byers *et al.* 2006), which could be used to restore fragile ecosystems that have been altered by human activities and take them to a desired state. Most restoration efforts try to improve the damaged abiotic environment in order to facilitate the subsequent colonisation by many species (Byers *et al.*, 2006). However, gorgonians are known to improve abiotic environment by themselves (Jones *et al.*, 1997; Buhl-Mortensen *et al.*, 2010) so using these organisms in the firsts stages of restoration processes would increase the ecological succession reducing costs and efforts (Byers *et al.*, 2006). As observed in this study, high gorgonian densities are capable to promote increases in the diversity, independently of the size of the colonies. This fact has important management applications, since no large organisms are required to successfully restore a marine benthic environment.

4.7. Future research

Similar studies in a wider range of habitats would be interesting to test the effects of gorgonian size and density in other regions. Tropical areas and cold regions, such as the North Atlantic, would be remarkable spots to carry out analogous experiments.

Furthermore, it would be interesting to carry out other experiments to test the possible effects of restoring degraded ecosystems with small-sized gorgonians, in order to corroborate the results obtained in this study.

Finally, it would also be challenging to determine which megafaunal organisms modify habitats in such a way that their presence becomes positive to other species, and hence, improves species richness and diversity. Therefore, identifying engineering species that facilitate colonisation and persistence of other taxa would be an important step forward in the field of conservation and restoration of benthic habitats.

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Appendix 1. Raw data of the variables used in the present study, for both transects of the Antarctic region. SU, sampling unit; D, gorgonian density; Size, gorgonian mean size; N, megafaunal abundance; H, Shannon-Wiener index (log2); expH, exponential of Shannon index; simp, Gini-Simpson index; invsimp, inverse of Simpson index; S, megafaunal species richness; epiN, epibiont abundance; epiS, epibiont species richness; NA, no available data.

Transect	SU	D	Size	N	H	expH	simp	invsimp	S	epiN	epiS
ANT_B3	ANT_B3_1	6.000	26.09111	37	3.49297	11.25874	0.89262	9.31293	14	9	3
ANT_B3	ANT_B3_2	0.667	14.19000	14	3.37878	10.40196	0.89796	9.80000	11	0	0
ANT_B3	ANT_B3_3	7.333	25.29000	28	3.62452	12.33357	0.90306	10.31579	15	5	3
ANT_B3	ANT_B3_4	4.667	27.68167	27	2.80196	6.97387	0.80384	5.09790	10	6	3
ANT_B3	ANT_B3_5	10.667	21.27400	58	3.28996	9.78088	0.85493	6.89344	15	9	3
ANT_B3	ANT_B3_6	2.000	34.66667	13	3.18083	9.06831	0.87574	8.04762	10	2	2
ANT_B3	ANT_B3_7	6.000	22.67889	28	2.67652	6.39312	0.78061	4.55814	10	6	2
ANT_B3	ANT_B3_8	6.667	29.05600	31	3.65211	12.57176	0.90739	10.79775	15	7	3
ANT_B3	ANT_B3_9	2.667	26.83000	40	3.66346	12.67102	0.88375	8.60215	19	4	2
ANT_B3	ANT_B3_10	5.333	23.20571	22	2.95854	7.77339	0.82645	5.76190	11	0	0
ANT_B3	ANT_B3_11	3.333	31.09600	27	3.75416	13.49323	0.90261	10.26761	17	4	2
ANT_B3	ANT_B3_12	10.000	25.79067	35	2.45678	5.48989	0.78367	4.62264	7	10	1
ANT_B3	ANT_B3_13	2.000	21.17943	14	2.89629	7.44510	0.85714	7.00000	8	1	1
ANT_B3	ANT_B3_14	2.667	26.17000	25	3.25366	9.53783	0.85120	6.72043	13	7	4
ANT_B3	ANT_B3_15	7.333	27.37364	25	3.20888	9.24635	0.86400	7.35294	12	6	2
ANT_B3	ANT_B3_16	2.667	25.65250	10	2.92193	7.57858	0.86000	7.14286	8	3	2
ANT_B3	ANT_B3_17	2.667	23.55500	14	2.98523	7.91851	0.85714	7.00000	9	2	2
ANT_B3	ANT_B3_18	2.667	27.53250	28	3.19006	9.12650	0.84439	6.42623	13	5	2
ANT_B3	ANT_B3_19	5.333	31.26375	36	3.23408	9.40922	0.86265	7.28090	13	5	1
ANT_B3	ANT_B3_20	2.667	31.47250	39	3.57077	11.88251	0.87574	8.04762	18	5	3
ANT_B3	ANT_B3_21	6.000	23.48667	35	3.35988	10.12519	0.88000	8.33333	13	5	2
ANT_B3	ANT_B3_22	2.000	21.11333	41	2.93260	7.63483	0.77335	4.41207	14	4	2
ANT_B3	ANT_B3_23	0.000	NA	23	3.08359	8.47720	0.86578	7.45070	10	NA	NA
ANT_B3	ANT_B3_24	0.00000	NA	26	2.59242	6.03108	0.76627	4.27848	9	NA	NA
ANT_B3	ANT_B3_25	0.00000	NA	11	2.00489	4.01357	0.71074	3.45714	5	NA	NA
ANT_B3	ANT_B3_26	0.00000	NA	8	2.40564	5.29870	0.78125	4.57143	6	NA	NA
ANT_B3	ANT_B3_27	0.00000	NA	18	3.61437	12.24711	0.90123	10.12500	14	NA	NA
ANT_B3	ANT_B3_28	1.33333	21.38500	13	2.35353	5.11075	0.73373	3.75556	7	0	0
ANT_B3	ANT_B3_29	0.00000	NA	20	3.30370	9.87446	0.87500	8.00000	12	NA	NA
ANT_B3	ANT_B3_30	0.66667	13.09000	23	2.66578	6.34569	0.76371	4.23200	10	0	0
ANT_B3	ANT_B3_31	0.00000	NA	21	3.36129	10.27662	0.85261	6.78462	14	NA	NA
ANT_B3	ANT_B3_32	0.66667	23.47000	19	3.26083	9.58533	0.88089	8.39535	11	0	0
ANT_B3	ANT_B3_33	0.00000	NA	13	2.66123	6.32570	0.82840	5.82759	7	NA	NA
ANT_B3	ANT_B3_34	0.66667	25.87000	45	2.52612	5.76019	0.74864	3.97839	9	0	0
ANT_B3	ANT_B3_35	0.00000	NA	69	2.18472	4.54637	0.68977	3.22343	10	NA	NA
ANT_B3	ANT_B3_36	1.33333	26.75500	51	2.72474	6.61042	0.80738	5.19162	10	0	0
ANT_B3	ANT_B3_37	0.00000	NA	56	1.96922	3.91556	0.62691	2.68034	8	NA	NA
ANT_B3	ANT_B3_38	0.00000	NA	46	3.08990	8.51439	0.77977	4.54077	17	NA	NA
ANT_B3	ANT_B3_39	1.33333	19.75500	38	2.50412	5.67303	0.75485	4.07910	9	0	0
ANT_B3	ANT_B3_40	2.66667	13.82250	50	2.72005	6.58898	0.80480	5.12295	10	0	0
ANT_B3	ANT_B3_41	0.66667	25.99000	24	3.09436	8.54074	0.84375	6.40000	12	0	0
ANT_B3	ANT_B3_42	2.00000	9.41000	9	3.16993	9.00000	0.88889	9.00000	9	1	1
ANT_B3	ANT_B3_43	0.66667	17.04000	22	3.29990	9.84845	0.88843	8.96296	11	0	0
ANT_B3	ANT_B3_44	0.00000	NA	27	3.15787	8.92512	0.87791	8.19101	10	NA	NA
ANT_B3	ANT_B3_45	0.00000	NA	19	3.22110	9.32496	0.85319	6.81132	12	NA	NA
ANT_B3	ANT_B3_46	0.00000	NA	23	3.41010	10.63022	0.88469	8.67213	13	NA	NA
ANT_B3	ANT_B3_47	2.00000	12.83000	41	1.86641	3.64624	0.54610	2.20315	9	0	0
ANT_B3	ANT_B3_48	0.00000	NA	27	2.72301	6.60250	0.73800	3.81675	12	NA	NA
ANT_B3	ANT_B3_49	0.00000	NA	50	3.36940	10.33453	0.85520	6.90608	17	NA	NA
ANT_B3	ANT_B3_50	0.66667	13.07000	46	3.33430	10.08611	0.82703	5.78142	18	0	0
ANT_B3	ANT_B3_51	0.00000	NA	21	2.79661	6.94808	0.82540	5.72727	9	NA	NA
ANT_B3	ANT_B3_52	0.00000	NA	29	2.75934	6.77086	0.75862	4.14286	12	NA	NA
ANT_B3	ANT_B3_53	0.66667	25.71000	40	2.65427	6.29530	0.76875	4.32432	10	0	0
ANT_B3	ANT_B3_54	0.00000	NA	25	3.09366	8.53659	0.83840	6.18812	12	NA	NA
ANT_B3	ANT_B3_55	1.33333	21.89500	105	2.34011	5.06341	0.60880	2.55623	18	1	1
ANT_B3	ANT_B3_56	0.00000	NA	126	1.47521	2.78024	0.43600	1.77306	11	NA	NA
ANT_B3	ANT_B3_57	1.33333	26.91500	31	2.74035	6.68233	0.79084	4.78109	10	2	1
ANT_B3	ANT_B3_58	2.66667	15.54750	64	2.29297	4.90063	0.60938	2.56000	15	9	3
ANT_B3	ANT_B3_59	8.66667	29.83769	44	3.67625	12.78382	0.88533	8.72072	19	4	2
ANT_B3	ANT_B3_60	3.33333	24.07800	31	3.47116	11.08978	0.89698	9.70707	13	5	1

Transect	SU	D	Size	N	H	expH	simp	invsimp	S	epiN	epiS
ANT_B3	ANT_B3_61	3.33333	24.50800	40	3.63321	12.40806	0.89250	9.30233	17	7	2
ANT_B3	ANT_B3_62	2.00000	30.23000	18	2.77995	6.86829	0.81481	5.40000	9	0	0
ANT_B3	ANT_B3_63	0.00000	NA	3	1.58496	3.00000	0.66667	3.00000	3	NA	NA
ANT_B3	ANT_B3_64	0.00000	NA	8	2.50000	5.65685	0.81250	5.33333	6	NA	NA
ANT_B3	ANT_B3_65	0.00000	NA	4	2.00000	4.00000	0.75000	4.00000	4	NA	NA
ANT_B3	ANT_B3_66	0.00000	NA	6	1.45915	2.74946	0.61111	2.57143	3	NA	NA
ANT_B3	ANT_B3_67	0.00000	NA	6	2.25163	4.76220	0.77778	4.50000	5	NA	NA
ANT_B3	ANT_B3_68	0.00000	NA	10	2.52193	5.74349	0.78000	4.54545	7	NA	NA
ANT_B3	ANT_B3_69	0.00000	NA	7	2.80735	7.00000	0.85714	7.00000	7	NA	NA
ANT_B3	ANT_B3_70	0.00000	NA	3	1.58496	3.00000	0.66667	3.00000	3	NA	NA
ANT_B3	ANT_B3_71	0.00000	NA	3	1.58496	3.00000	0.66667	3.00000	3	NA	NA
ANT_B5	ANT_B5_1	6.00000	NA	30	3.35119	10.20490	0.87111	7.75862	14	2	1
ANT_B5	ANT_B5_2	7.33333	NA	24	3.27206	9.66021	0.87153	7.78378	12	1	1
ANT_B5	ANT_B5_3	6.00000	NA	15	3.00624	8.03467	0.86222	7.25806	9	0	0
ANT_B5	ANT_B5_4	6.66667	NA	17	3.45482	10.96491	0.89965	9.96552	12	0	0
ANT_B5	ANT_B5_5	4.66667	NA	17	3.57247	11.89653	0.90657	10.70370	13	2	1
ANT_B5	ANT_B5_6	6.00000	NA	19	3.00311	8.01728	0.81994	5.55385	11	0	0
ANT_B5	ANT_B5_7	5.33333	NA	13	3.18083	9.06831	0.87574	8.04762	10	1	1
ANT_B5	ANT_B5_8	4.66667	NA	25	2.55963	5.89555	0.70400	3.37838	11	1	1
ANT_B5	ANT_B5_9	6.66667	NA	27	2.67900	6.39479	0.73800	3.81675	11	0	0
ANT_B5	ANT_B5_10	9.33333	NA	36	3.79537	13.88419	0.90895	10.98305	18	0	0
ANT_B5	ANT_B5_11	6.00000	NA	28	2.33688	5.05211	0.75510	4.08333	7	0	0
ANT_B5	ANT_B5_12	19.33333	17.12500	204	3.41757	10.68540	0.78830	4.72372	32	5	2
ANT_B5	ANT_B5_15	3.33333	17.04200	12	2.58496	6.00000	0.80556	5.14286	7	0	0
ANT_B5	ANT_B5_16	4.00000	13.80000	13	3.18083	9.06831	0.87574	8.04762	10	1	1
ANT_B5	ANT_B5_17	6.66667	18.26400	21	2.78401	6.88765	0.83447	6.04110	8	2	1
ANT_B5	ANT_B5_18	1.33333	18.74500	8	2.40564	5.29870	0.78125	4.57143	6	0	0
ANT_B5	ANT_B5_19	4.66667	22.44429	8	3.00000	8.00000	0.87500	8.00000	8	0	0
ANT_B5	ANT_B5_20	0.66667	10.36000	5	2.32193	5.00000	0.80000	5.00000	5	0	0
ANT_B5	ANT_B5_21	2.66667	18.91500	16	3.25000	9.51366	0.87500	8.00000	11	0	0
ANT_B5	ANT_B5_22	4.00000	15.36667	6	2.25163	4.76220	0.77778	4.50000	5	2	1
ANT_B5	ANT_B5_23	4.66667	14.45143	8	2.75000	6.72717	0.84375	6.40000	7	1	1
ANT_B5	ANT_B5_24	6.66667	13.87200	9	2.72548	6.61381	0.83951	6.23077	7	1	1
ANT_B5	ANT_B5_25	1.33333	14.83500	5	2.32193	5.00000	0.80000	5.00000	5	0	0
ANT_B5	ANT_B5_37	0.00000	NA	22	0.69986	1.62434	0.24380	1.32240	3	NA	NA
ANT_B5	ANT_B5_38	0.00000	NA	6	0.65002	1.56919	0.27778	1.38462	2	NA	NA
ANT_B5	ANT_B5_40	0.00000	NA	34	2.25745	4.78146	0.65917	2.93401	9	NA	NA
ANT_B5	ANT_B5_41	0.66667	18.06000	15	1.87160	3.65939	0.60444	2.52809	6	0	0
ANT_B5	ANT_B5_42	0.66667	12.56000	22	2.97057	7.83848	0.81818	5.50000	11	0	0
ANT_B5	ANT_B5_43	2.66667	9.91000	42	2.67547	6.38848	0.70295	3.36641	14	0	0
ANT_B5	ANT_B5_44	7.33333	14.55364	34	3.67646	12.78569	0.91003	11.11538	15	0	0
ANT_B5	ANT_B5_45	0.66667	17.75000	33	2.13687	4.39806	0.60973	2.56235	10	0	0
ANT_B5	ANT_B5_46	0.00000	NA	12	3.02206	8.12324	0.86111	7.20000	9	NA	NA
ANT_B5	ANT_B5_47	2.00000	12.38000	36	2.56849	5.93190	0.74691	3.95122	10	0	0
ANT_B5	ANT_B5_48	0.00000	NA	23	2.45558	5.48535	0.72590	3.64828	9	NA	NA
ANT_B5	ANT_B5_49	3.33333	15.74000	52	2.16246	4.47679	0.58284	2.39716	12	0	0
ANT_B5	ANT_B5_50	1.33333	18.58000	24	1.43456	2.70300	0.50694	2.02817	5	1	1
ANT_B5	ANT_B5_51	4.66667	15.29429	30	1.99137	3.97615	0.57778	2.36842	9	0	0
ANT_B5	ANT_B5_52	6.00000	15.38333	36	3.11328	8.65350	0.83951	6.23077	12	0	0
ANT_B5	ANT_B5_53	3.33333	19.13000	46	2.77132	6.82732	0.75520	4.08494	13	0	0
ANT_B5	ANT_B5_54	3.33333	13.69600	32	2.00161	4.00448	0.58594	2.41509	9	0	0
ANT_B5	ANT_B5_55	0.66667	14.16000	15	2.36560	5.15366	0.78222	4.59184	6	0	0
ANT_B5	ANT_B5_56	0.66667	18.69000	16	2.21692	4.64899	0.65625	2.90909	8	0	0
ANT_B5	ANT_B5_57	0.66667	14.02000	2	1.00000	2.00000	0.50000	2.00000	2	0	0
ANT_B5	ANT_B5_58	0.66667	10.38000	21	2.16333	4.47949	0.68027	3.12766	7	0	0
ANT_B5	ANT_B5_59	3.33333	22.61000	24	3.08496	8.48528	0.83333	6.00000	12	0	0
ANT_B5	ANT_B5_60	2.66667	15.92000	23	2.27250	4.83159	0.68809	3.20606	8	0	0
ANT_B5	ANT_B5_61	2.00000	19.81333	19	3.05030	8.28385	0.85873	7.07843	10	0	0
ANT_B5	ANT_B5_62	0.00000	NA	33	2.39392	5.25585	0.64830	2.84334	12	NA	NA
ANT_B5	ANT_B5_63	0.00000	NA	38	1.83724	3.57325	0.54709	2.20795	8	NA	NA
ANT_B5	ANT_B5_64	1.33333	14.44000	14	2.41380	5.32876	0.75510	4.08333	7	0	0
ANT_B5	ANT_B5_65	0.66667	8.85000	23	1.17319	2.25509	0.37429	1.59819	5	0	0
ANT_B5	ANT_B5_66	2.00000	12.84667	32	1.49878	2.82603	0.42773	1.74744	8	0	0
ANT_B5	ANT_B5_67	2.00000	14.68333	128	1.08361	2.11933	0.30701	1.44302	9	0	0
ANT_B5	ANT_B5_68	1.33333	17.01000	24	1.29085	2.44673	0.42014	1.72455	5	0	0

Appendix 2. Raw data of the variables used in the present study, for both transects of the Mediterranean region. SU, sampling unit; D, gorgonian density; Size, gorgonian mean size; N, megafaunal abundance; H, Shannon-Wiener index (log2); expH, exponential of Shannon index; simp, Gini-Simpson index; invsimp, inverse of Simpson index; S, megafaunal species richness; epiN, epibiont abundance; epiS, epibiont species richness; NA, no available data.

Transect	SU	D	size	N	H	expH	simp	invsimp	S	epiN	epiS
Med1	Med1_0000	0.667	6.560	6	1.45915	2.74946	0.61111	2.57143	3	0	0
Med1	Med1_0005	0.667	2.670	15	2.25656	4.77852	0.78222	4.59184	5	0	0
Med1	Med1_0010	2.667	3.160	16	2.14678	4.42839	0.71875	3.55556	6	0	0
Med1	Med1_0015	1.333	3.465	12	2.58496	6.00000	0.80556	5.14286	7	0	0
Med1	Med1_0020	0.000	NA	7	1.44882	2.72984	0.61224	2.57895	3	NA	NA
Med1	Med1_0025	6.000	6.363	6	1.79248	3.46410	0.66667	3.00000	4	0	0
Med1	Med1_0030	24.000	5.351	8	2.75000	6.72717	0.84375	6.40000	7	4	1
Med1	Med1_0035	17.333	6.656	14	2.69238	6.46379	0.80612	5.15789	8	5	3
Med1	Med1_0040	14.000	7.050	22	3.20255	9.20582	0.85124	6.72222	12	3	3
Med1	Med1_0045	18.000	7.548	19	3.22110	9.32496	0.87535	8.02222	11	2	2
Med1	Med1_0050	19.333	7.999	43	2.73740	6.66865	0.80151	5.03815	10	4	2
Med1	Med1_0055	5.333	7.034	4	1.50000	2.82843	0.62500	2.66667	3	0	0
Med1	Med1_0060	19.333	6.677	24	2.84436	7.18188	0.83333	6.00000	9	2	1
Med1	Med1_0065	25.333	9.674	34	2.55027	5.85743	0.73010	3.70513	11	2	2
Med1	Med1_0070	17.333	8.398	16	2.42379	5.36581	0.77344	4.41379	7	0	0
Med1	Med1_0075	27.333	5.803	23	3.93618	15.30764	0.92628	13.56410	17	6	1
Med1	Med1_0080	22.667	5.285	41	3.53295	11.57509	0.88043	8.36318	16	5	4
Med1	Med1_0085	10.000	5.419	21	3.23210	9.39636	0.87528	8.01818	11	3	2
Med1	Med1_0090	21.333	6.607	32	3.31512	9.95292	0.87500	8.00000	13	4	3
Med1	Med1_0095	15.333	5.515	49	3.41629	10.67590	0.85881	7.08260	17	2	2
Med1	Med1_0100	22.000	5.494	34	3.34866	10.18699	0.87889	8.25714	13	3	2
Med1	Med1_0105	12.000	6.022	48	2.54742	5.84587	0.73611	3.78947	13	4	4
Med1	Med1_0110	17.333	8.969	36	3.67968	12.81430	0.88889	9.00000	18	5	4
Med1	Med1_0115	26.000	7.803	67	3.16007	8.93874	0.82914	5.85267	17	3	2
Med1	Med1_0120	8.000	9.944	25	2.75508	6.75092	0.78720	4.69925	10	1	1
Med1	Med1_0125	8.000	7.734	15	2.87291	7.32539	0.85333	6.81818	8	0	0
Med1	Med1_0130	6.667	6.576	10	3.12193	8.70551	0.88000	8.33333	9	1	1
Med1	Med1_0135	0.667	4.230	4	0.81128	1.75477	0.37500	1.60000	2	0	0
Med1	Med1_0140	2.000	7.797	25	3.58928	12.03592	0.90240	10.24590	14	1	1
Med1	Med1_0145	7.333	4.875	8	2.50000	5.65685	0.81250	5.33333	6	0	2
Med1	Med1_0150	14.667	7.712	47	3.80270	13.95492	0.90539	10.56938	19	3	0
Med1	Med1_0155	5.333	5.374	5	1.92193	3.78929	0.72000	3.57143	4	0	0
Med1	Med1_0160	6.667	6.064	59	3.57946	11.95435	0.86814	7.58388	19	0	0
Med1	Med1_0165	3.333	6.056	13	3.18083	9.06831	0.87574	8.04762	10	0	0
Med1	Med1_0170	0.667	2.730	25	3.34760	10.17955	0.87040	7.71605	13	0	0
Med1	Med1_0175	8.000	5.806	31	3.78437	13.77871	0.91779	12.16456	16	4	1
Med1	Med1_0180	9.333	4.964	26	3.81123	14.03767	0.91124	11.26667	17	1	1
Med1	Med1_0185	6.667	3.505	43	3.40941	10.62514	0.87399	7.93562	15	0	0
Med1	Med1_0190	4.667	3.232	31	2.80809	7.00356	0.79917	4.97927	10	0	0
Med1	Med1_0195	9.333	3.449	36	3.21664	9.29617	0.85031	6.68041	13	2	2
Med1	Med1_0200	6.000	3.327	24	2.99060	7.94805	0.85764	7.02439	9	0	0
Med1	Med1_0205	22.667	4.464	32	3.49950	11.30979	0.88672	8.82759	15	1	1
Med1	Med1_0210	14.667	3.489	40	3.85306	14.45058	0.91000	11.11111	19	4	3
Med1	Med1_0215	2.667	3.433	12	2.75163	6.73477	0.81944	5.53846	8	0	0
Med1	Med1_0220	2.667	5.675	20	3.10869	8.62602	0.85000	6.66667	11	0	0
Med1	Med1_0225	2.000	2.303	32	3.06955	8.39511	0.84766	6.56410	12	0	0
Med1	Med1_0230	0.000	NA	26	2.65033	6.27809	0.81065	5.28125	8	NA	NA
Med1	Med1_0235	0.000	NA	29	2.23633	4.71196	0.72057	3.57872	8	NA	NA
Med1	Med1_0240	0.000	NA	40	2.51387	5.71148	0.78625	4.67836	8	NA	NA
Med1	Med1_0245	0.667	6.790	10	2.04644	4.13085	0.72000	3.57143	5	0	0
Med1	Med1_0250	0.000	NA	38	1.91117	3.76114	0.60111	2.50694	7	NA	NA
Med1	Med1_0255	0.000	NA	20	1.37095	2.58641	0.56000	2.27273	3	NA	NA
Med1	Med1_0260	1.333	2.400	26	1.86296	3.63754	0.67160	3.04505	5	0	0
Med1	Med1_0265	0.000	NA	43	2.61576	6.12945	0.81341	5.35942	8	NA	NA
Med1	Med1_0270	0.667	1.880	32	2.33156	5.03351	0.73633	3.79259	8	0	0
Med1	Med1_0275	0.667	6.950	30	1.60044	3.03236	0.52444	2.10280	6	0	0
Med1	Med1_0280	1.333	1.345	6	1.91830	3.77976	0.72222	3.60000	4	0	0
Med1	Med1_0285	6.000	3.698	21	3.23686	9.42738	0.86168	7.22951	12	0	0
Med1	Med1_0290	1.333	4.115	6	1.45915	2.74946	0.61111	2.57143	3	0	0
Med1	Med1_0295	0.667	2.120	33	2.73413	6.65356	0.81726	5.47236	9	0	0

Transect	SU	D	size	N	H	expH	simp	invsimp	S	epiN	epiS
Med1	Med1_0300	0.667	2.190	26	3.06470	8.36692	0.82840	5.82759	12	0	0
Med1	Med1_0305	2.667	3.608	32	2.56593	5.92136	0.79883	4.97087	8	0	0
Med1	Med1_0310	2.667	3.485	59	3.35749	10.24958	0.86412	7.35941	17	0	0
Med1	Med1_0315	3.333	2.744	57	3.44030	10.85507	0.87842	8.22532	16	0	0
Med1	Med1_0320	6.000	3.410	19	3.11058	8.63729	0.85319	6.81132	11	0	0
Med1	Med1_0325	8.000	4.432	27	3.20399	9.21502	0.87243	7.83871	11	2	1
Med1	Med1_0330	6.667	2.197	25	3.12322	8.71328	0.84800	6.57895	12	0	0
Med1	Med1_0335	5.333	6.365	13	2.10391	4.29873	0.74556	3.93023	5	2	2
Med2	Med2_0105	2.667	5.508	2	1.00000	2.00000	0.50000	2.00000	2	0	0
Med2	Med2_0110	2.667	7.070	8	2.50000	5.65685	0.81250	5.33333	6	1	1
Med2	Med2_0115	4.000	7.928	4	0.81128	1.75477	0.37500	1.60000	2	0	0
Med2	Med2_0120	5.333	9.148	7	2.23593	4.71065	0.77551	4.45455	5	1	1
Med2	Med2_0125	5.333	5.145	2	1.00000	2.00000	0.50000	2.00000	2	0	0
Med2	Med2_0130	1.333	5.340	4	1.00000	2.00000	0.50000	2.00000	2	0	0
Med2	Med2_0135	2.000	5.063	5	1.52193	2.87175	0.64000	2.77778	3	0	0
Med2	Med2_0140	6.667	5.651	14	2.41380	5.32876	0.75510	4.08333	7	0	0
Med2	Med2_0145	9.333	10.272	5	1.37095	2.58641	0.56000	2.27273	3	4	3
Med2	Med2_0150	0.667	6.940	3	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0155	2.667	4.205	9	2.41938	5.34942	0.79012	4.76471	6	0	0
Med2	Med2_0160	1.333	3.005	6	0.65002	1.56919	0.27778	1.38462	2	0	0
Med2	Med2_0165	0.000	NA	3	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0170	0.667	5.490	5	1.92193	3.78929	0.72000	3.57143	4	0	0
Med2	Med2_0175	5.333	8.468	10	2.84644	7.19223	0.84000	6.25000	8	0	0
Med2	Med2_0180	4.667	7.050	11	2.66353	6.33583	0.82645	5.76190	7	0	0
Med2	Med2_0185	4.000	9.497	4	1.50000	2.82843	0.62500	2.66667	3	1	1
Med2	Med2_0190	2.000	2.400	6	1.79248	3.46410	0.66667	3.00000	4	0	0
Med2	Med2_0195	0.667	7.230	2	1.00000	2.00000	0.50000	2.00000	2	0	0
Med2	Med2_0200	0.667	2.570	6	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0205	5.333	8.189	12	1.62581	3.08616	0.62500	2.66667	4	1	1
Med2	Med2_0210	4.000	10.790	2	1.00000	2.00000	0.50000	2.00000	2	0	0
Med2	Med2_0215	2.000	13.225	8	0.95443	1.93782	0.46875	1.88235	2	0	0
Med2	Med2_0220	0.667	4.180	9	0.50326	1.41741	0.19753	1.24615	2	0	0
Med2	Med2_0225	1.333	5.910	10	2.12193	4.35275	0.74000	3.84615	5	0	0
Med2	Med2_0230	4.000	9.105	6	1.45915	2.74946	0.61111	2.57143	3	1	1
Med2	Med2_0235	6.000	12.002	7	1.66450	3.17003	0.61224	2.57895	4	0	0
Med2	Med2_0240	0.667	11.580	4	1.50000	2.82843	0.62500	2.66667	3	0	0
Med2	Med2_0245	10.000	15.357	11	2.73216	6.64449	0.84298	6.36842	7	6	4
Med2	Med2_0250	7.333	11.914	14	2.61058	6.10748	0.81633	5.44444	7	1	1
Med2	Med2_0255	6.000	10.431	14	2.12809	4.37137	0.71429	3.50000	6	3	3
Med2	Med2_0260	7.333	13.150	7	1.84237	3.58599	0.69388	3.26667	4	3	2
Med2	Med2_0265	1.333	1.235	5	1.37095	2.58641	0.56000	2.27273	3	0	0
Med2	Med2_0270	1.333	10.365	8	1.50000	2.82843	0.62500	2.66667	3	0	0
Med2	Med2_0275	4.000	9.460	3	1.58496	3.00000	0.66667	3.00000	3	0	0
Med2	Med2_0280	3.333	5.282	8	1.75000	3.36359	0.65625	2.90909	4	0	0
Med2	Med2_0285	1.333	3.415	2	1.00000	2.00000	0.50000	2.00000	2	0	0
Med2	Med2_0290	4.667	7.365	3	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0295	3.333	10.592	6	2.58496	6.00000	0.83333	6.00000	6	1	1
Med2	Med2_0300	2.000	6.240	1	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0305	3.333	6.122	4	0.81128	1.75477	0.37500	1.60000	2	2	1
Med2	Med2_0310	0.000	NA	9	1.87996	3.68066	0.64198	2.79310	5	0	0
Med2	Med2_0315	0.667	5.940	3	0.91830	1.88988	0.44444	1.80000	2	0	0
Med2	Med2_0320	1.333	1.710	3	1.58496	3.00000	0.66667	3.00000	3	0	0
Med2	Med2_0325	0.667	6.590	3	1.58496	3.00000	0.66667	3.00000	3	0	0
Med2	Med2_0330	1.333	3.220	4	1.50000	2.82843	0.62500	2.66667	3	0	0
Med2	Med2_0335	2.000	15.635	8	2.50000	5.65685	0.81250	5.33333	6	1	1
Med2	Med2_0340	2.000	NA	6	1.79248	3.46410	0.66667	3.00000	4	2	2
Med2	Med2_0345	0.000	NA	3	1.58496	3.00000	0.66667	3.00000	3	0	0
Med2	Med2_0350	0.667	6.870	10	1.57095	2.97100	0.58000	2.38095	4	0	0
Med2	Med2_0355	12.000	13.366	20	1.78150	3.43783	0.63000	2.70270	5	2	1
Med2	Med2_0360	10.667	13.035	20	3.30370	9.87446	0.87500	8.00000	12	7	4
Med2	Med2_0365	0.667	16.600	5	1.37095	2.58641	0.56000	2.27273	3	0	0
Med2	Med2_0370	0.000	NA	7	1.37878	2.60049	0.57143	2.33333	3	0	0
Med2	Med2_0375	0.667	NA	2	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0380	0.000	NA	5	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0385	0.000	NA	7	1.55666	2.94171	0.65306	2.88235	3	0	0
Med2	Med2_0390	0.000	NA	4	1.50000	2.82843	0.62500	2.66667	3	0	0
Med2	Med2_0395	2.000	5.640	7	1.55666	2.94171	0.65306	2.88235	3	0	0
Med2	Med2_0400	0.000	NA	9	0.99108	1.98767	0.49383	1.97561	2	0	0

Transect	SU	D	size	N	H	expH	simp	invsimp	S	epiN	epiS
Med2	Med2_0405	0.000	NA	11	1.30930	2.47821	0.52893	2.12281	3	0	0
Med2	Med2_0410	0.667	4.930	9	0.98643	1.98127	0.37037	1.58824	3	0	0
Med2	Med2_0415	0.000	NA	14	1.42991	2.69430	0.53061	2.13043	4	0	0
Med2	Med2_0420	0.000	NA	9	0.50326	1.41741	0.19753	1.24615	2	0	0
Med2	Med2_0425	0.667	5.220	5	0.00000	1.00000	0.00000	1.00000	1	0	0
Med2	Med2_0430	0.667	8.330	14	1.57442	2.97815	0.61224	2.57895	4	0	0
Med2	Med2_0435	2.000	3.673	7	1.84237	3.58599	0.69388	3.26667	4	0	0
Med2	Med2_0440	9.333	13.492	10	2.92193	7.57858	0.86000	7.14286	8	0	0
Med2	Med2_0445	3.333	16.053	5	1.52193	2.87175	0.64000	2.77778	3	1	1