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Title

Temporal variability in epifaunal assemblages associated with temperate gorgonian gardens

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Abstract

The present study is one of the few that investigate the temporal variability of epifaunal assemblages associated with coral species, particularly the octocorals *Eunicella gazella* and *Leptogorgia lusitanica* in south Portugal. The results suggest time rather than colony size as a primary driver of the ecological patterns of these assemblages, which were dominated by amphipods, molluscs and polychaetes. Temporal variability was linked to changes in environmental parameters, namely temperature, chlorophyll *a* and particulate organic carbon. Hence, temporal variability must be taken into account for the design of future biodiversity assessment studies, as different patterns may be observed depending on the sampling time. Associated epifaunal assemblages were consistently dominated by resident species (i.e. species present in all sampling periods) and a peak of rare species was observed in the transition from spring to summer following the increase of seawater temperature. Turnover was particularly high in the transition between the spring and summer periods. In both hosts, turnover was higher in the small sized colonies, which generally harboured less diverse and less abundant assemblages which also differed from those inhabiting larger size colonies. The high levels of diversity associated with gorgonian colonies highlights the need for the conservation of this priority habitat.

1. Introduction

Gorgonian gardens, like coral reefs, may provide an array of goods and ecological services, conferring to them a high relevance in the context of coastal ecosystems. Among those products and services are several bioactive compounds that can be valuable for human (e.g. anti-tumoral, anti-inflammatory; Bhakuni and Rawat, 2005; Berrue and Kerr, 2009; Rocha et al., 2011) and environmental health (e.g. anti-fouling agents). They can also support local tourism activities, as gorgonian gardens are

appreciated diving spots. Their ecological and social relevance, particularly in temperate ecosystems, along with the increasing threats to the marine environment makes the protection of gorgonian gardens a priority.

Marine Protected Areas (MPAs) have been increasingly used to ensure the protection of habitats with particular ecological values (Kelleher and Kenchington, 1999).

According to the International Union for Conservation of Nature (IUCN), an MPA is defined as: “Any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment”

(Resolution 17.38 of the IUCN General Assembly, 1988). MPAs can provide several benefits, such as management of fisheries, contribution to sound scientific data, maintenance of ecosystem services, education opportunities, increase of financial capital through tourism and preservation of species and genetic diversity (IUCN, 1994). However, an increase in the tourism industry tends to intensify recreational activities such as diving (Coma et al., 2004). Physical contacts by divers caused either by accidental kicks by fins, or climbing (Davenport and Davenport, 2006), can impact gorgonians causing possible detachment, loss of tissue and consequent overgrowth by epibionts (Medio et al., 1997; Jameson et al., 1999; Tratalos and Austin, 2001; Lloret and Riera, 2008). Recently, an effort was made to recognize the conservation value of coral gardens, including gorgonian-dominated biocenoses in south Portugal and Spain, by their inclusion in the OSPAR (Convention for the Protection of the Marine Environment of the North-East Atlantic) list of protected habitats (Anonymous, 2011). However, the shallow sublittoral coastal rocky habitats of the Algarve coast in southern Portugal have been poorly studied (but see Gonçalves et al., 2008, 2010; Cúrdia et al., 2013; Carvalho et al., 2014). Therefore, a better understanding of these

marine habitats and the communities they support, as well as the mapping of their habitat distribution is needed for the establishment of efficient MPAs.

Gorgonian ecosystems present abundant and rich biotic assemblages (Gonçalves et al., 2008, 2010; Carvalho et al., 2014). The deep infralittoral and especially the circalittoral rocky areas are dominated by dense gorgonian gardens formed by different species (mainly *Eunicella labiata*, *Eunicella verrucosa*, *Eunicella gazella*, *Leptogorgia sarmentosa* and *Leptogorgia lusitanica*) (Gonçalves et al., 2010; Cúrdia et al., 2013). Some studies of the epibenthic assemblages inhabiting gorgonian colonies in temperate regions (Patton, 1972; Wendt et al., 1985; Greene, 2008; Carvalho et al., 2014) showed biodiversity values similar to those reported in tropical and sub-tropical areas (Spotte et al., 1995; Goh et al., 1999; Kumagai and Aoki, 2003; Buhl-Mortensen and Mortensen, 2005). To our knowledge, no study has been undertaken addressing the temporal variability in the ecological patterns of benthic fauna associated with gorgonian gardens. However, the only study we found addressing this topic in scleractinian species, *Astroides calycularis* (Terrón-Sigler et al., 2014) reports a significant contribution of time in shaping the structure of associated macrofaunal assemblages. Quantifying temporal changes in epibenthic communities associated with gorgonians will further strengthen our understanding of ecosystem and biodiversity changes and contribute to a better knowledge of existing ecological patterns. The distribution of species inhabiting coral reefs is often heterogeneous (Henry et al., 2009), so we can expect a similar trend within gorgonian gardens, as different species have different ecological requirements.

By assessing the spatial and temporal variability of the associated epifaunal assemblages of gorgonian species, the present study adds valuable information to the ecological patterns related to these particularly rich and sensitive environments.

Increasing the information available will improve the ability to accurately monitor and manage the ecosystem in the future. Our hypothesis is that epibenthic fauna inhabiting the gorgonian colonies of *Eunicella gazella* and *Leptogorgia lusitanica* of southern Portugal are affected by the temporal fluctuations in seawater temperature and productivity, using chlorophyll *a* (chl *a*) as a proxy. This study aims to assess: i) whether these assemblages are maintained over time; and ii) whether the biological descriptors (number of *taxa*, abundance, expected number of species) and assemblage structure are related to temporal environmental variability (e.g. temperature and chl *a*).

2. Material and Methods

2.1. Study area and sampling strategy

The present study was undertaken in Pedra da Greta, a rocky outcrop in the central-south of Portugal (Algarve), located at 15-18 m depth, parallel to the coast. The outcrop was 3.6 km length, ranging from 20 to 90 m in width, and from 1 to 3.5 m in height.

The sampling design included the delimitation of two sampling areas (PGW and PGE) separated by more than one kilometre. *Leptogorgia lusitanica* Stiasny, 1937 and *Eunicella gazella* Studer, 1878, were selected as study subjects as they are the two most abundant gorgonians in the area (Cúrdia et al., 2013). There have been some discussions regarding the taxonomic validity of *L. lusitanica* and in some cases it is considered as a variant of *L. sarmentosa* (Esper, 1789) (<http://www.marinespecies.org/aphia.php?p=taxdetails&id=759104>). However, as in the south of Portugal the authors observed that both *L. lusitanica* and *L. sarmentosa* occupy different ecological niches, we decide to use *L. lusitanica* until further

clarifications on the taxonomy. Three colony sizes were defined (small, medium and large), according to the size frequency distribution of each species (Cúrdia et al., 2013). For *Eunicella gazella* the height ranges were: small, <9 cm; medium, 9–17 cm; large >17 cm; and for *Leptogorgia lusitanica*: small, <10 cm; medium, 10–30 cm; large, >30 cm. Details on the morphological differences between these gorgonian species, as well as in gorgonian assemblages are given in Cúrdia et al. (2013) and Carvalho et al. (2014). Three replicates of each colony size and species (3 colonies x 3 sizes x 2 sites x 2 species) were collected by hand during scuba diving in July and November 2010 and March, June and August 2011 (180 colonies in total). During the dive, the samples were placed individually in closed plastic bags. The colonies were preserved in 96% ethanol until further laboratory processing.

2.2. Laboratory analyses

Colony parameters (i.e. maximum height and width) were measured in the laboratory. Photographs of each colony were taken and analysed using the image analysis software, ImageJ (Schneider et al., 2012) to estimate the colony surface area and perimeter. The number of colony branches was calculated by analysing skeleton binary images using the ImageJ plugin AnalyzeSkeleton (Arganda-Carreras et al., 2010). The preserved samples were washed over a 100 μ m mesh and kept in 96% ethanol. The identification of the macrofauna was carried out using a stereoscopic microscope (Olympus SZX 12) and a microscope (Leitz Laborlux S). Because of the large amount of samples, high diversity observed and lack of taxonomy expertise, it was impossible to dedicate the same identification effort to every group (the full list of taxa is provided as supplementary material, Table S1). A list of reference works used in the identification of epifaunal organisms is also provided as supplementary material (S2).

2.3. Environmental variables

Environmental data were used to relate seasonal patterns to community changes, namely sea surface temperature (SST; °C), chlorophyll *a* (mg m⁻³), photosynthetically available radiation (PAR; Einstein m⁻² d⁻¹) and particulate organic carbon (POC; mg m⁻³). The annual pattern of variability for each environmental variable was based on the average value for each month. Data on SST was gathered from the oceanographic buoy located $\approx$ 2 nautical miles from the study area (www.hidrografico.pt/boias-ondografo.php). Chlorophyll *a*, PAR and POC were derived from satellite remote sensing data, collected from the Giovanni online data system (MODIS-Aqua 4 km, monthly processed data, available at <http://disc.sci.gsfc.nasa.gov/giovanni/overview/index.html>), developed and maintained by the NASA Goddard Environmental Sciences Data and Information Services Center - GES DISC (Acker and Leptoukh, 2007).

2.4. Data analyses

The classical biological indices number of taxa (S), abundance (N), Pielou's evenness (*J'*) (Pielou (1969) and Hurlbert's expected species richness (Hurlbert, 1971) ($ES_{(n)}$) were calculated and used to describe biodiversity patterns and to assess changes in the structure of epibenthic assemblages associated with gorgonians. The Hurlbert's expected number of species was calculated in the present study because of the different sizes of the samples. As being rarefied to the same number of individuals, it provides an adequate estimate of biodiversity when samples have different sizes. A three-way analysis of variance (ANOVA) was carried out to test for differences in those univariate variables in relation to time (five levels, fixed), site (two levels, random) and size (three levels, fixed).

149 β -diversity was analysed in terms of turnover (differences between consecutive
150 months), based on the following expression:

$$t = \frac{l + g}{S \times ci}$$

151 where, l is the number of species lost, g is the number of species gained, S is the total
152 number of species present and ci is the census interval (months) (Diamond and May,
153 1977).

154 Changes in assemblage structure were assessed by an analysis of similarities using
155 permutational multivariate analyses of variances (PERMANOVA) based on the Bray-
156 Curtis similarity matrix, after log (x+1) transformation of the data. Specifically, the
157 design addressed the factors time (five levels, fixed), site (two levels, random) and
158 size (three levels, fixed) for each gorgonian separately and tested the null hypothesis
159 of no significant differences regarding any of the factors on the composition and
160 structure of the associated assemblages.

161 In order to better understand the temporal dynamics of the associated epifaunal
162 assemblages, the samples of all colonies were pooled for each month, and the
163 occurrence of each taxon during the study period was analysed and *taxa* classified
164 into three categories (Piló et al., in press): i) residents, *taxa* present during all
165 sampling dates; ii) occasional, *taxa* present in three or four sampling dates; and iii)
166 rare, *taxa* present in only one or two dates.

167 The relationship between assemblage structure and predictor environmental variables
168 (sea surface temperature, chlorophyll a , particulate organic carbon and photosynthetic
169 active radiation) and variables of colony attributes (area, width, number of branches)
170 was analysed by a distance-based redundancy analysis (dbRDA) (McArdle and
171 Anderson, 2001), as this method provides the flexibility to choose the dissimilarity

index to be used. For each gorgonian species, data were also analysed separately for each size class to minimize the scale effects related to colony size. This methodology preserves the primary focus on the variation of gorgonian-associated fauna over time but also taking into account colony characteristics at small scales. Particulate organic carbon (POC) and chlorophyll *a* (chl *a*) data were highly skewed, but chl *a* was more even after transformation (log 10), whereas transformed POC data were still skewed. What is more, these two variables were highly correlated ($r=0.97$, $P<0.001$, Pearson product-moment correlation coefficient). Therefore, for the dbRDA analysis, only photosynthetic active radiation (PAR), temperature and chl *a* (log 10 transformed) were used. For the purpose of this analysis, we used the average values of each of the variables during the week of each sampling period. As for the gorgonian colony attributes, the area of the colony is highly correlated to height, width, perimeter and number of branches (*Eunicella gazella*: $r = 0.75-0.88$, $P<0.01$; *Leptogorgia lusitanica*: $r = 0.85-0.95$, $P<0.01$). All morphometric variables were normally distributed, and there was no need to transform them. However, to prevent co-linearity effects only three variables were retained for the analysis: area, width and number of branches. PRIMER v6 software (Clarke and Gorley, 2006) and the open source software R version 12.1 (R Development Core Team, 2011) were used to carry out data analyses.

3. Results

3.1. Physico-chemical variability in the water column

The sea surface temperature (SST) showed a clear seasonal pattern, reaching minimum values in January-March (15.9°C) and peaking in August (23.8°C; Figure 1). Chl *a* generally peaked in March (8.7 mg m⁻³; Figure 1), while PAR increased gradually towards a peak in June-July (60.1 Einstein m⁻² d⁻¹), and then decreased to its minimum in December 2010 (14.6 Einstein m⁻² d⁻¹). The concentration of organic

particulates (POC) increased drastically in March 2010 (668.4 mg m^{-3}), and then it abruptly declined in April 2010 (163.3 mg m^{-3}). Afterwards, the POC value kept relatively constant up to November 2010 ($61.2\text{-}98.4 \text{ mg m}^{-3}$), whilst in March 2011 another peak (although lower than the previous year, 271.0 mg m^{-3}) was observed (Figure 1).

3.2. Associated epibenthic assemblages

In the present study, 178 *taxa* were identified from a total of 19204 individuals collected in 180 gorgonian colonies (129 *taxa* in *Eunicella gazella* and 155 in *Leptogorgia lusitanica*).

3.2.1. Spatial-temporal and colony size variability

Eunicella gazella's associated assemblages

Except for June 2011, when Canalipalpata polychaetes were numerically dominant, the epifaunal assemblages associated with *Eunicella gazella* were numerically dominated by crustaceans and Platyhelminthes. This increase in the abundance of polychaetes is mainly due to an abrupt increase in the number of *Filograna implexa* in a single replicate, which strongly affects the rarefied biodiversity observed in this month (Figure 2). Arthropods (mainly amphipods), polychaetes and molluscs were the most diverse groups throughout the study period. The analysis of the *taxa* contributing to more than 60% of the total abundance per sampling period showed that specimens of the class Ostracoda and Platyhelminthes und. dominated throughout the sampling period (Table 1). The amphipod *Erichthonius punctatus* was also highly abundant, except for July 2010 and March 2011 (Table 1).

In general, species richness and abundance were higher during late spring and summer with minimum values observed in March, irrespectively of the colony size

(Table 2). The three-way ANOVA results indicated a significant interaction for the term time x site x size. Overall, a significant temporal variation between autumn-winter and spring-summer months was detected for abundance and for the number of *taxa*. In the latter case, values observed in August were also significantly higher compared to June and July (Table 3). On the other hand, significantly lower values of equitability and expected number of species were found in June, particularly when compared to those observed in March (Tables 2, 3). When the factor size was significant, a general increasing pattern from small to medium-large colonies was observed, except for equitability, which showed the opposite trend (Table 3). According to the PERMANOVA analysis (Table 4), the composition and structure of the associated assemblages significantly differed in time. March and November showed different patterns compared to the summer sampling periods (Table 4). Resident species numerically dominated the associated assemblages, except for June, when rare species presented the highest abundance (Tables 1, 5). This exception resulted from the massive colonization of the polychaete (*Filograna implexa*) on a single large colony. November 2010 presented the highest dominance of resident species, accounting for 91% of total abundance (Table 5). The abundance of occasional *taxa* was higher in late spring and summer, while rare species (44 *taxa*) largely contributed to the peak of *taxa* richness observed in August (total of 89 *taxa*) (Table 5).

Leptogorgia lusitanica's associated assemblages

The associated fauna of *Leptogorgia lusitanica* was numerically dominated by crustaceans in all sampling occasions except for November 2010, when molluscs, namely gastropods, predominated. This exception is due to the increase in abundance of *Simnia spelta* in a single replicate. Similarly to the pattern observed in *Eunicella*

gazella, polychaetes, molluscs and crustaceans were the most diverse groups throughout the study period.

Species of the family Tritoniidae and the class Ostracoda were always present among the *taxa* contributing to more than 60% of the total abundance per sampling occasion (except Ostracoda in November 2010 and tritoniids in March 2011) (Table 1). Additionally, *Simnia spelta* also dominated the samples of November 2010 and March and August 2011 (Table 1).

For the number of individuals, species richness, Pielou's equitability, and for the expected number of *taxa*, the highest values were generally recorded in summer (July or August) and the lowest were found in November 2010 (Table 2). The results of the three-way ANOVA confirmed the existence of significant temporal variation for all the biological descriptors except for abundance (Table 5). In the later case, only size was a significant factor, with smaller colonies harbouring fewer organisms than medium and these fewer than large colonies (Table 5). For the number of *taxa* and the expected number of species, the ANOVA confirmed significantly depressed numbers in November in comparison with the summer months (July and August) and in the case of the number of *taxa*, also with March. For both indices, lower values were observed in small colonies compared with medium and/or large colonies but this pattern was not spatially consistent. Equitability was also lower in November than in all the other sampling periods (Table 5).

The comparison between rarefaction curves shows some degree of complementarity in the assemblages along the year, as the pooled number of species of each month was always lower than the grand total (Figure 2). On the other hand, the lowest slope of the ES curve observed for November 2010 confirmed this month as the one contributing the least to the overall biodiversity (Figure 3). The PERMANOVA

(Table 4) indicated that composition and structure of associated epifaunal assemblages differed significantly between most of the study periods in both sampling sites.

Although the number of residents was higher in July 2010 (1741 individuals), the highest relative abundance occurred in November 2010 (90%), similar to that observed for *Eunicella gazella*'s associated assemblages. On the other hand, both total and relative abundance were lowest in June 2011 (360 individuals and 38%, respectively) (Table 6). The highest relative abundance of occasional *taxa* occurred in June 2011 (58%, 33 different *taxa*). The lowest values for number of *taxa* (12), total (37) and relative abundance (5%) were observed in November 2010. All variables studied for rare *taxa* presented highest values in July (N – 179, %TN – 6%, S - 42) and lowest in June 2011 (N – 29, %TN – 3%, S - 12) (Table 6).

3.2.2. β -diversity as turnover

Turnover values for faunal composition of *Eunicella gazella* associated assemblages were generally below 20% irrespectively of the colony size, except for the spring-summer transition (June to August), where turnover was above 30% (Figure 3). Except for the period from November to March, the assemblages of small-sized colonies showed higher turnover values than those inhabiting medium- and large-sized colonies (Figure 3). The same general patterns were detected on the associated assemblages of *Leptogorgia lusitanica*. Maximum turnover values were observed in the transition from June to August, regardless of the colony size.

3.3. Relationships between biological and environmental data

The dbRDA analyses performed explains over 30% of the variation for the *Eunicella gazella* data, and 50% for the *Leptogorgia lusitanica* data, regardless of the size class.

In general, the environmental parameters (especially PAR, but also chl *a* for *Eunicella gazella* and temperature for *Leptogorgia lusitanica*) together with colony attributes (number of branches, area and width) all contributed significantly to explaining the patterns of the associated fauna (Table 7).

The ordination diagrams for *Eunicella gazella* data generally separate the samples from November and March from the remaining sampling occasions. This separation mainly results from the lower values of temperature and PAR during the autumn-winter months (Figure 4). In *Leptogorgia lusitanica* dbRDA analysis, November samples formed a clear cluster, mainly due to lower values of both temperature and PAR, but also due to the area and the number of branches of the colony (Figure 4).

4. Discussion

The studied epifaunal assemblages associated with *Eunicella gazella* and *Leptogorgia lusitanica* encompass a broad spectrum of *taxa* (178 *taxa*; the value is underestimated as some organisms could not be identified to the species level). Most *taxa* belonged to Crustacea (mainly amphipods), Polychaeta and Mollusca. The dominance of those three taxonomic groups is in accordance with recent studies targeting a shallow water scleractinian (*Cladocora caespitosa*) in the Mediterranean Sea (Terrón-Sigler et al., 2014) and studies targeting assemblages associated with other invertebrate (Garcia et al., 2008) and algal species (e.g. Sánchez-Moyano et al., 2000; Torres et al., 2015). However, it differs from the patterns reported for deep-sea gorgonians, where brittle-stars were dominant (Buhl-Mortensen et al., 2010). The high diversity values observed are in agreement with data on gorgonian gardens from the study area (Carvalho et al., 2014; Cúrdia et al., 2015) and other regions (Goh et al., 1999; Greene, 2008; Kumagai and Aoki, 2003). Specimens of the phylum Platyhelminthes, apparently belonging to a single species, were very abundant and exclusively

associated with *Eunicella gazella* colonies. This pattern has been previously suggested as a strategy to avoid predation as those flatworms are white coloured similar to the colour of the *Eunicella gazella* branches (Carvalho et al., 2014). A tritoniid species (Mollusca: Nudibranchia) and the gastropod *Simnia spelta* consistently associated with both *E. gazella* and *Leptogorgia lusitanica*, and seem to have a close dependence with these particular habitats. The association of these *taxa* has been previously reported, as they are well-known octocoral predators (Oliverio et al., 2009; García-Matucheski and Muniain, 2011). Therefore, this relationship may be disrupted if the gorgonian gardens' degrade, with consequences for the populations of both predator species. Indeed, although the whole assemblages are relevant and need to be considered, the existence of exclusive species within these environments (and the knowledge of these relationships) is of utmost importance especially when considering the scenario of global warming and the increasing disturbance pressure that coastal zones have been experiencing. However, taking into account the almost non-existent knowledge on the contribution of each species to ecosystem functioning, no species should be disregarded. By losing alpha diversity, we will eventually be losing beta diversity, and negatively impacting the ecosystem's key functional traits (Chapin et al., 2000).

There is a general lack of studies regarding the distribution, abundance, community structure and dynamics of invertebrate assemblages associated with gorgonian gardens (along with scleractinian corals and other invertebrate hosts). However, that information is crucial for conservation and management of sensitive coastal habitats. Information concerning the temporal variability associated with these putative patterns is even scarcer, thus limiting comparative analyses (Kumagai and Aoki, 2003; also see Terrón-Sigler et al., 2014 for scleractinian corals). However, previous

studies on the associated fauna of other species-forming habitats, such as macroalgae, seagrass meadows, and scleractinian corals showed a clear temporal/seasonal variability pattern (Guidetti and Bussotti, 2000; Guerra-García et al., 2011; Terrón-Sigler et al., 2014).

Temporal patterns of the epibenthic non-colonial invertebrate assemblages associated with the studied gorgonian species were generally consistent in both hosts. Species richness, abundance, and the expected number of *taxa* showed a temporal variation, with generally higher values observed in the spring – summer months (i.e. July 2010, June and August 2011) and lower values recorded in the autumn-winter sampling periods (i.e. November 2010 and March 2011). Only Pielou's evenness showed the reverse trend, as a result of an abundance peak observed for some species, such as *Caprella fretensis* and *Filograna implexa*, in the spring-summer period. However, it is worth noting that this peak of abundance mainly results from a single colony replicate. These general patterns match the ones observed in the macroalgae or seagrass-associated peracarid fauna both in the Strait of Gibraltar (south Spain; Guerra-García et al., 2010, 2011), NW Iberian Peninsula (Esquete et al., 2010), and also in soft-bottom fauna of other temperate areas (van Hoey et al., 2007). But they contrast to what has been reported from the Mediterranean (Delgado et al., 2009; Terron-Sigler et al., 2014 - for density only) or NE Atlantic coastal lagoons (Carvalho et al., 2011), where the peak of abundance and diversity mainly occurred during autumn-winter or winter-spring periods. This disparity probably results from differences in water temperature (Coma et al., 2000); different dynamics in coastal and transitional ecosystems, as the latter are much more influenced by human-induced eutrophication and subsequent oxygen depletion as well as changes in nutrient availability that occur mainly during summer (Pereira et al., 2010).

The temporal variability pattern also indicated that higher turnover rates (i.e. changes in the number of *taxa* between two consecutive times) were consistently observed for the spring-summer periods, following the increase in seawater temperature. In cold and temperate seas, marine organisms show life cycles with marked seasonal patterns (generally with an increase in activity and abundance in spring-summer and a decrease in winter), which has been linked to seawater temperature and food availability (Coma et al., 2000) and agrees with our findings. However, temperature may have direct and indirect effects on other physical and biological parameters (namely food availability), and consequently it has been difficult to disentangle the relative contribution of food availability and temperature on the dynamics of marine communities (Coma et al., 2000 and references therein). Even though there might be more factors linked to these general patterns (e.g. predation and competition – Coma et al., 2000; food nutritional value - Danovaro et al., 1997), several studies have suggested that food availability could have as high a contribution as temperature in determining seasonality in benthic suspension feeders (Coma et al., 1998; Ribes et al., 1999). The spring-summer period also corresponded to the maximum in diversity and abundance, which followed the peak of phytoplankton observed in March 2011. Enhanced food availability following the phytoplankton peak has been reported by several authors (Buchanan and Moore, 1986; Costa and Costa, 1999; Rees et al., 2007; McArthur et al., 2010; Schückel et al., 2010). The dbRDA analysis indicated that the temporal variability of epibenthic-associated assemblages is significantly influenced by most of the environmental variables included in the model (seawater temperature, chlorophyll *a* and photosynthetic active reaction). However, morphometric attributes of the gorgonians (e.g. colony area) also play a relevant role in the general ecological patterns, as highlighted previously (Cúrdia et al., 2015). The

present study confirmed the colony size as a predictor of both the biological indices and the structure of the assemblages, as differences were detected between small and medium and/or large colonies. Complexity of the colony in both gorgonians, measured as a fractal dimension, was not, however, a determinant for the ecological patterns of variation and consequently it was not considered in the present study. In other foundation species (e.g. macroalgae and plants) the role of habitat complexity in structuring associated assemblages varies. Complexity has been shown to have a significant contribution to the ecological patterns of associated assemblages (Tuya et al 2011) and to contribute to abundance patterns of the associated assemblages (but not as much as the quantity of the habitat; Torres et al., 2015). However others could not find any significant relationships (Attrill et al., 2000; Taniguchi et al., 2003).

Turnover reflects a dynamic equilibrium between immigration and extinctions and, therefore, is likely to reflect the changes in the life cycles of species throughout the year. In this context, the highest turnover observed during the transition from June to August due to an increase in the number of species mainly due to the contribution of many occasional and rare *taxa*. The occasional and rare taxa were mainly observed during the spring and summer with the winter assemblages consisting mainly of resident *taxa*. Another interesting result was the highest turnover rates in small size colonies of both species during this spring-summer transition. In a previous meta-analysis of species turnover in zooplankton communities, Shurin et al. (2007) showed that at the same latitudes more diverse systems were associated with decreased turnover rates. This result matches the patterns observed in the present study as the small-size colonies for both species were generally associated with depressed diversity compared to their medium-large size counterparts.

419 Although the total number of *taxa* identified in this study was 132 for *Eunicella*
 420 *gazella* and 156 for *Leptogorgia lusitanica*, the highest species richness (S) per
 421 colony was 55 and 45, respectively. In general, only a few *taxa* accounted for the
 422 majority of the abundance of the assemblages associated with each host. Most of
 423 these *taxa* were classified as residents, i.e. *taxa* that were present in all sampling
 424 dates, and among these, Nematoda, Sipunculida, the polychaetes *Syllidia armata*, the
 425 bivalve *Hiatella arctica*, the gastropods Tritoniidae and *Simnia spelta*, the amphipods
 426 *Erichthonius punctatus*, *Ischyrocerus inexpectatus*, *Gammaropsis* cf. *crenulata* and
 427 *Lembos* cf. *websteri*, the isopods *Astacilla* sp. and the tanaid aff. *Leptochelia savignyi*
 428 were common to both gorgonian species. With the exception of the well-known
 429 gorgonian predators *Simnia spelta*, and the Tritoniidae (even though the latter could
 430 not be identified to species level), the remaining *taxa* are commonly observed in
 431 different habitats, especially (but not restricted to) artificial reefs and vegetated
 432 habitats (Sánchez-Jerez et al., 1999; Bradshaw et al., 2003; Boaventura et al., 2006;
 433 Carvalho et al., 2007, 2012; Moura et al., 2008; Bedini et al., 2011). Some of those
 434 species have also been reported as dominant in epifaunal assemblages associated with
 435 other invertebrate hosts, such as *Leptochelia savignyi* with the tunicate *Microcosmus*
 436 *sabatieri* (Voultsiadou et al., 2007). The relatively high number of resident *taxa* (20 in
 437 *Eunicella gazella* and 23 in *Leptogorgia lusitanica*) together with their high
 438 abundance also indicates that the assemblages are dominated by a “core” group of
 439 species during the year, and this is reflected in relatively low turnover rates (*Eunicella*
 440 *gazella*, 11.5-22.1%; *Leptogorgia lusitanica*, 10.4-34.8%). Previous studies
 441 concerning the reproductive cycles of benthic non-colonial invertebrates in Portugal
 442 showed that several species have continuous reproduction (despite one or two
 443 seasonal reproductive peaks) (Pardal et al., 2000; Malaquias and Sprung, 2005),

which may support the maintenance of stable populations of “core” assemblages that persist throughout the year. The PERMANOVA results suggest a high degree of temporal variability, expressed by the existence of significant differences between all pairs of sampling occasions analysed. However, and despite this variability, the proximity of the samples collected in July 2010 and August 2011 in the multivariate analyses suggest that there is an annual cyclicality in the composition and structure of the faunal assemblages associated with gorgonians.

The present study suggests that the fauna associated with gorgonians is shaped by the morphometric parameters of gorgonian colonies. The effect of colony size has been previously reported for gorgonians (Carvalho et al., 2014; Cúrdia et al., 2015) and also for coral species (e.g. Bos and Hoeksema, 2014). Besides, the current results show an apparent temporal variation linked to environmental parameters, namely temperature and chlorophyll *a*. This result is relevant especially with the current scenario of global sea temperature rises and nutrient enrichment, which have been shown to affect the dynamics and biomass of phytoplankton and zooplankton communities (e.g. Norderhaug et al., 2015; Lefort et al., 2015; Rice et al., 2015). If we continue disregarding these habitats, future changes in the ecosystem functioning cannot be identified due to the lack of baseline data. In order to support the conservation of these habitats, further studies focusing on the biodiversity changes across spatial and temporal scales are needed to increase our understanding of dynamics associated with gorgonian gardens. Despite the dominance of resident *taxa*, these habitats harbour rich and sustained assemblages and consequently their degradations will result in a great loss of biodiversity.

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Figure captions

Figure 1. Values of sea surface temperature (SST), chlorophyll *a*, photosynthetic active reaction (PAR) and particulate organic carbon (POC) from January 2010 to December 2011 in Pedra da Greta, south Portugal.

Figure 2. Rarefaction curves (Hurlbert's expected number of species) in *Eunicella gazella* (EG) and *Leptogorgia lusitanica* (LL) assemblages for different colony size classes and sampling times. S, small; M, medium; L, large.

Figure 3. Turnover in *Eunicella gazella* and *Leptogorgia lusitanica* assemblages for different colony size classes. S, small; M, medium; L, large. See text for further clarifications.

Figure 4. Distance based Redundancy analysis (dbRDA) ordination biplot for July (Jul), November (Nov), March (Mar), June (Jun) and August (Aug) samples. The vector lines represent the relationship of environmental data (seawater temperature, temp; irradiance, par; chlorophyll *a*, chl_a) and colonies attributes (area, width and no. of branches) to the ordination axes; their length is proportional to their relative significance.

Table 1. Species contributing to more than 60% of abundance per sampling period for *Eunicella gazella* and *Leptogorgia lusitanica*.

R, residents; O, occasional; Ra, rare (see text for further details).

July 2010		November		March 2011		June		August	
<i>Eunicella gazella</i>									
Turbellaria	R	<i>Erichthonius punctatus</i>	R	Turbellaria	R	Turbellaria	R	Turbellaria	R
Ostracoda	R	Turbellaria	R	aff. <i>Leptochelia savygni</i>	R	Ostracoda	R	<i>Erichthonius punctatus</i>	R
Bivalvia sp. 1	O	Ostracoda	R	<i>Gammaropsis</i> cf. <i>crenulata</i>	R	<i>Gammaropsis</i> cf. <i>crenulata</i>	R	Ostracoda	R
<i>Hiatella arctica</i>	R	<i>Simnia spelta</i>	R	<i>Ischerocerus inexpectatus</i>	R	<i>Erichthonius punctatus</i>	R	<i>Musculus</i> sp. 1	O
Tritoniidae	R	<i>Gammaropsis</i> cf. <i>crenulata</i>	R	Ostracoda	R	<i>Ischerocerus inexpectatus</i>	R	<i>Gammaropsis</i> cf. <i>crenulata</i>	R
<i>Phtisica marina</i>	R			Phyllodocidae	O			Tritoniidae	R
<i>Musculus</i> sp. 1	O							Bivalvia sp. 1	O
								aff. <i>Leptochelia savygni</i>	R
<i>Leptogorgia lusitanica</i>									
<i>Caprella fretensis</i>	R	<i>Simnia spelta</i>	R	Ostracoda	R	Ostracoda	R	Ostracoda	R
Ostracoda	R	Tritoniidae	R	<i>Ischerocerus inexpectatus</i>	R	<i>Gammaropsis</i> cf. <i>crenulata</i>	R	Tritoniidae	R
<i>Ischerocerus inexpectatus</i>	R			<i>Simnia spelta</i>	R	Tritoniidae	R	<i>Erichthonius punctatus</i>	R
<i>Astacilla</i> sp.	R			<i>Astacilla</i> sp.	R	<i>Ischerocerus inexpectatus</i>	R	<i>Gammaropsis</i> cf. <i>crenulata</i>	R
<i>Gammaropsis</i> cf. <i>crenulata</i>	R			<i>Erichthonius punctatus</i>	R	<i>Corynactis viridis</i>	O	<i>Simnia spelta</i>	R
<i>Hiatella arctica</i>	R			<i>Gammaropsis</i> cf. <i>crenulata</i>	R	<i>Astacilla</i> sp.	R	Bivalvia sp. 1	R
<i>Phtisica marina</i>	R			<i>Syllidia armata</i>	R	<i>Phtisica marina</i>	Ra	<i>Astacilla</i> sp.	R
Tritoniidae	R					<i>Caprella fretensis</i>	R	<i>Phtisica marina</i>	Ra
								<i>Hiatella arctica</i>	R
								<i>Modiolus</i> sp.	O

Table 2. Abundance and biodiversity data on the attendant faunal assemblages of *Eunicella gazella* and *Leptogorgia lusitanica* per colony size (Sm – small; M – medium; L – large) and time. n – number of colonies; N - number of individuals per colony; S - number of taxa per colony; J' - Pielou's evenness; $ES_{(100)}$ - Hurlbert's expected number of species per 100 individuals.

		<i>Eunicella gazella</i>					<i>Leptogorgia lusitanica</i>			
		n	N	S	J'	$ES_{(100)}$	N	S	J'	$ES_{(100)}$
Sm	July 2010	6	92	22	0.86	-	306	27	0.73	17.18
	November	6	153	22	0.70	18.13	97	14	0.44	-
	March 2011	6	39	19	0.90	-	105	27	0.82	26.32
	June	6	371	27	0.40	13.88	53	13	0.82	-
	August	6	395	31	0.63	17.67	246	34	0.75	22.96
M	July 2010	6	670	38	0.70	19.01	1343	79	0.70	27.32
	November	6	356	27	0.58	14.47	167	12	0.30	9.67
	March 2011	6	76	28	0.87	-	382	34	0.64	18.31
	June	6	755	36	0.44	13.18	113	40	0.92	38.15
	August	6	687	55	0.61	23.10	320	62	0.82	36.02
L	July 2010	6	363	45	0.69	25.51	1126	60	0.51	19.17
	November	6	301	36	0.62	20.54	500	44	0.39	18.74
	March 2011	6	192	32	0.67	23.40	597	49	0.75	23.84
	June	6	6887	50	0.22	7.31	772	57	0.69	25.99
	August	6	702	73	0.69	31.22	1038	75	0.71	28.44
	Sm	30	1050	60	0.56	20.53	807	63	0.71	24.03
	M	30	2544	85	0.56	21.39	2325	111	0.71	31.21
	L	30	8445	110	0.32	13.70	4033	127	0.64	28.06
	July 2010	18	1125	63	0.67	23.37	2775	96	0.63	25.24
	November	18	810	54	0.56	18.94	764	51	0.35	17.57
	March 2011	18	307	50	0.71	28.60	1084	66	0.70	24.64
	June	18	8013	66	0.28	8.73	938	68	0.70	28.88
	August	18	1784	89	0.61	26.89	1604	96	0.71	30.89
	Total	90	12039	132	0.43	17.33	7165	156	0.65	30.08

Table 3. Summary of results of a three-way ANOVA for univariate data for *Eunicella gazella*. S, small; M, medium; L, large. Jul, July 2010; Nov, November 2010; Mar, March 2011; Jun, June 2011; Aug, August 2011. $ES_{(100)}$, Hurlbert's expected number of species. *, $p < 0.05$; **, $p < 0.01$.

Source	df	No. of taxa		Post-hocs		
		MS	F	Time	Size	
Time, Ti	4	2.4697	8.89*	Site GW	Jul, GE	S<M
Site, Si	1	0.074	0.36	M Mar<Nov=Jun=Jul=Ago	Jun, GW	S<L
Size, Sz	2	2.4905	4.79		Mar, GE	S<M=L
Ti x Si	4	0.2778	1.37	Site GE		
Ti x Sz	8	0.1076	0.21	M Nov<Jul=Ago		
Si x Sz	2	0.5204	2.56	S Mar<Nov=Jun=Jul=Ago		
Ti x Si x Sz	8	0.5128	2.52*			
RES	60	0.2034				
TOT	90					
No. of individuals						
Time, Ti	4	13.6612	78.05***	Site GW		
Site, Si	1	0.0063	0.01	L Mar=Nov=Jul=Ago<Jun	Jul, GE	S<L=M
Size, Sz	2	12.0371	6.92	M Mar<Jul=Ago=Nov=Jun	Jun, GW	S=M<L
Ti x Si	4	0.175	0.3		Mar, GE	S<M=L
Ti x Sz	8	1.2497	0.96	Site GE		
Si x Sz	2	1.7398	2.95	M Mar=Nov<Ago=Jul=Jun		
Ti x Si x Sz	8	1.2954	2.2*	S Mar<Jul=Nov=Ago=Jun		
RES	60	0.5899				
TOT	90					
Pielou's equitability						
Time, Ti	4	0.2367	14.12*	L Jun<Nov=Jul=Mar=Ago	Jun	L<M=S
Site, Si	1	0.0214	0.56	M Jun=Ago=Nov=Jul<Mar	Mar	S<L<M
Size, Sz	2	0.04	1.07	S Mar<Nov,Ago,Jul		
Ti x Si	4	0.0168	0.44	Ago=Jun<Jul		
Ti x Sz	8	0.1186	8.1**			
Si x Sz	2	0.0375	0.98			
Ti x Si x Sz	8	0.0147	0.38			
RES	60	0.0381				
TOT	90					
$ES_{(100)}$						
Time, Ti	4	2.1274	10.09*	Ago>Jun=Mar		
Site, Si	1	0.0885	0.44			
Size, Sz	2	1.6331	5.03			
Ti x Si	4	0.2109	1.05			
Ti x Sz	8	0.2188	0.55			
Si x Sz	2	0.3244	1.62			
Ti x Si x Sz	8	0.397	1.98			
RES	60	0.2007				
TOT	90					

Table 4. Results of the main and pair-wise tests of PERMANOVA on the assemblages associated with each gorgonian.

Source	df	<i>Eunicella gazella</i>		<i>Leptogorgia lusitanica</i>	
		MS	Pseudo-F	MS	Pseudo-F
Time, Ti	4	8015.7	3.8663**	18713	5.444**
Site, Si	1	1194.5	0.53088	1940.5	0.96631
Size, Sz	2	5559.8	4.9193	9157.6	3.6643
TixSi	4	2073.2	0.92142	3437.4	1.7117***
TixSz	8	1875.2	1.3074	3207.2	1.3973
SixSz	2	1130.2	0.50232	2499.1	1.2445
TixSixSz	8	1434.3	0.63745	2295.3	1.143
Res	30	2250		2008.2	
Total	59				

Pair-wise tests					
<i>Term "Time"</i>			<i>Term "Time x Site"</i>		
Groups	t		GW		
Jul, Mar	2.4013*		Groups	t	
Jul, Nov	2.455*		Jul, Aug	1.7587***	
Aug, Mar	2.7935*		Jul, Jun	1.6443**	
			Jul, Mar	2.132***	
			Jul, Nov	3.5088***	
			Aug, Jun	1.7771**	
			Aug, Mar	2.0827***	
			Aug, Nov	3.0471***	
			Jun, Mar	1.7424***	
			Jun, Nov	2.8432***	
			Mar, Nov	2.4412***	
			GE		
			Groups	t	
			Jul, Aug	1.9079**	
			Jul, Jun	1.6804**	
			Jul, Mar	1.6302**	
			Jul, Nov	3.8027***	
			Aug, Jun	1.7694**	
			Aug, Mar	1.9713***	
			Aug, Nov	2.7031***	
			Jun, Nov	3.3502***	
			Mar, Nov	3.2454***	

Table 5. Summary of results of a three-way ANOVA for univariate data for *Leptogorgia lusitanica*. S, small; M, medium; L, large. Jul, July 2010; Nov, November 2010; Mar, March 2011; Jun, June 2011; Aug, August 2011. $ES_{(100)}$, Hurlbert's expected number of species. *, $p < 0.05$; **, $p < 0.01$. *, $p < 0.05$; **, $p < 0.01$.

No. of taxa				Post-hocs		
Source	df	MS	F	Time	Size	
Time, Ti	4	4.1065	12.21*	Nov<Mar=Ago=Jul	GW	S<M<L
Site, Si	1	0.0001	0		GE	S<M=L
Size, Sz	2	7.0329	10.67			
Ti x Si	4	0.3362	1.81			
Ti x Sz	8	0.3175	1.33			
Si x Sz	2	0.6589	3.54*			
Ti x Si x Sz	8	0.239	1.28			
RES	60	0.1862				
TOT	90					

No. of individuals						
Time, Ti	4	4.7965	5.39			S<M<L
Site, Si	1	0.3931	0.68			
Size, Sz	2	23.3475	88.55*			
Ti x Si	4	0.8899	1.53			
Ti x Sz	8	0.7975	0.91			
Si x Sz	2	0.2637	0.45			
Ti x Si x Sz	8	0.8783	1.51			
RES	60	0.5801				
TOT	90					

Pielou's equitability						
Time, Ti	4	0.4387	11.04*	Nov<Jul=Mar=Ago=Jun		
Site, Si	1	0.0172	0.86			
Size, Sz	2	0.1094	3.72			
Ti x Si	4	0.0397	1.99			
Ti x Sz	8	0.0255	0.66			
Si x Sz	2	0.0294	1.47			
Ti x Si x Sz	8	0.0385	1.93			
RES	60	0.019				
TOT	90					

$ES_{(100)}$						
Time, Ti	4	410.1819	11.92*	Nov<Jul=Ago		
Site, Si	1	2.1965	0.08			
Size, Sz	2	728.9664	3.95			
Ti x Si	4	34.4028	1.32			
Ti x Sz	8	41.026	2.03			
Si x Sz	2	184.3202	7.05**			
Ti x Si x Sz	8	20.1692	0.77			
RES	60	26.1525				
TOT	90					

Table 6. Total abundance (N), relative abundance (%TN) and number of taxa (S) of resident, occasional and rare species for *Eunicella gazella* and *Leptogorgia lusitanica* attendant assemblage during the sample period.

	<i>Eunicella gazella</i>									<i>Leptogorgia lusitanica</i>								
	Residents			Occasional			Rare			Residents			Occasional			Rare		
	N	%TN	S	N	%N	S	N	%N	S	N	%N	S	N	%N	S	N	%N	S
July 2010	809	72%	20	268	24%	25	48	4%	18	1741	63%	23	855	31%	31	179	6%	42
November	740	91%	20	46	6%	19	24	3%	15	689	90%	23	37	5%	12	38	5%	16
March 2011	236	77%	20	59	19%	20	12	4%	10	771	71%	23	264	24%	27	49	5%	16
June	2300	29%	20	118	1%	31	5594	70%	15	360	38%	23	546	58%	33	29	3%	12
August	1361	76%	20	259	15%	25	164	9%	44	1011	63%	23	513	32%	34	80	5%	39

Table 7. Results of the distance-based redundancy analysis (dbRDA) for the fitted model relating a set of variables (morphometrical: colony area, width and number of branches; environmental: chl *a*, PAR and temperature), where amounts explained by each set added to the model is conditional on sets of variables already in the model. % Var: percentage of variance in species data explained by that set of variables and Cum. %: cumulative percentage of variance explained.

		<i>Eunicella gazella</i>			<i>Leptogorgia lusitanica</i>		
	Parameters	% Var	Cum(%)	<i>F</i>	% Var	Cum(%)	<i>F</i>
S	Area	17.41	17.4	1.79*	8.67	8.67	1.22ns
	Width	23.33	40.7	2.40**	5.64	14.31	0.79ns
	no. branches	8.03	48.8	0.83ns	17.10	31.41	2.39**
	Chl <i>a</i>	19.00	67.8	1.96*	12.67	44.08	1.77ns
	PAR	17.77	85.5	1.83*	27.91	71.99	3.90**
	Temperature	14.43	100	1.49ns	28.00	99.99	3.91*
M	Area	16.49	16.5	1.83*	6.45	6.45	1.06ns
	Width	13.82	30.3	1.54ns	9.73	16.18	1.60ns
	no. branches	12.27	42.6	1.36ns	11.00	27.17	1.80*
	Chl <i>a</i>	25.07	67.7	2.79**	10.17	37.34	1.66ns
	PAR	16.39	84.0	1.82*	45.33	82.68	7.42**
	Temperature	15.98	100	1.78*	17.33	100.01	2.84**
L	Area	8.41	8.4	0.81ns	15.34	15.34	2.04*
	Width	12.98	21.4	1.25ns	20.08	35.42	2.67**
	no. branches	7.85	29.2	0.75ns	10.73	46.15	1.43ns
	Chl <i>a</i>	22.27	51.5	2.14**	15.24	61.39	2.03*
	PAR	31.74	83.2	3.05***	24.30	85.69	3.24**
	Temperature	16.74	100	1.61ns	14.30	99.99	1.91*

Highlights

- Sampling period was a primary driver of the ecological patterns with higher diversity and abundance observed in spring and summer months
- Temporal variability was linked to changes in environmental parameters, (temperature and chlorophyll *a*)
- Assemblages associated with *Eunicella gazella* and *Leptogorgia lusitanica* gorgonians were consistently dominated by resident taxa
- Rare species increased from spring to summer following the increase of seawater temperature
- Turnover rate was higher from June to August and in small size gorgonian colonies which are also less diverse