REDUCING THE DATA-DEFICIENCY OF THREATENED EUROPEAN HABITATS: SPATIAL VARIATION OF SABELLARIID WORM REEFS AND ASSOCIATED FAUNA IN THE SICILY CHANNEL, MEDITERRANEAN SEA

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ABSTRACT

Biogenic reefs, such as those produced by tube-dwelling polychaetes of the genus *Sabellaria*, are valuable marine habitats which are a focus of protection according to European legislation. The achievement of this goal is potentially hindered by the lack of essential empirical data, especially in the Mediterranean Sea. This study addresses some of the current knowledge gaps by quantifying and comparing multi-scale patterns of abundance and distribution of two habitat-forming species (*Sabellaria alveolata* and *S. spinulosa*) and their associated fauna along 190 km of coast on the Italian side of the Sicily Channel. While the abundance of the two sabellariids and the total number of associated taxa did not differ at any of the examined scales (from tens of centimetres to tens-100 of kilometres), the structure (composition in terms of both the identity and the relative abundance of constituting taxa) of the associated fauna and the abundance of several taxa (the polychaetes *Eulalia ornata*, *Syllis pulvinata*, *S. garciai*, *Nereis splendida* and *Arabella iricolor*, and the amphipods *Apolochus neapolitanus*, *Tethylembos viguieri* and *Caprella acanthifera*) varied among locations established ~50-100 km apart. *Syllis pulvinata* also showed significant variation between sites (hundreds of metres apart), analogously to the other syllid polychaetes *S. armillaris* and *S. gracilis*, the nereidid polychaete *Nereis rava*, and the amphipod *Gammaropsis ulrici*. The largest variance of *S. spinulosa*, of the structure of the whole associated fauna and of 56% of taxa analysed individually occurred at the scale of replicates (metres apart), while that of the dominant bio-constructor *S. alveolata* and of 25% of taxa occurred at the scale of sites. The remaining 19% and the total richness of taxa showed the largest variance at the scale of locations. Present findings contribute to meet a crucial requirement of any future effective protection strategy, i.e., identifying relevant scales of variation to be included in protection schemes aiming at preserving representative samples not only of target habitats and organisms, but also of the processes driving such variability.

Keywords: Biogenic reef; ecosystem engineer; endangered habitat; *Sabellaria alveolata*; *Sabellaria spinulosa*; spatial scale; species interaction; subtidal

1. Introduction

Organisms known as bio-constructors produce three-dimensional structures providing habitats to a large diversity of sessile and mobile species (e.g., Jones et al., 1994). Besides the most notable case represented by cnidarians, such as hermatypic corals (Sheppard et al., 2009), several other animal taxa have such an ability, including sponges (Bell et al., 2013), molluscs (Gutiérrez et al., 2003), polychaetes (Naylor and Viles, 2000) and bryozoans (Wood et al., 2012). Gregarious tube-dwelling worms of the Sabellaridae family (Annelida), such as for example *Phragmatopoma californica* in California and *Gunnarea capensis* in South Africa, can form, provided suitable environmental conditions, extensive reefs (Achary, 1974). According to the Habitats Directive definition, reefs can be defined as "s*ubmarine, or exposed at low tide, rocky substrates and biogenic concretions, which arise from the sea floor in the sublittoral zone but may extend into the littoral zone where there is an uninterrupted zonation of plant and animal communities. These reefs generally support a zonation of benthic communities of algae and animal species including concretions, encrustations and corallogenic concretions*" (European Commission DG Environment, 2003). Along the European coasts, the honeycomb worms *Sabellaria alveolata* and *S. spinulosa* form the most important sabellariid bio-constructions. These can develop in the intertidal and shallow subtidal zone as encrusting formations adhering to rocks, ball-shaped ('hummocks') structures or large banks (Wilson, 1971; Dubois et al., 2002, 2006; Desroy et al., 2011), whose 'reefiness' can be quantified based on a number of physical and biological characteristics (Hendrick and Foster-Smith, 2006). Sabellariid constructions are not only found on natural substrates, but also on artificial structures (Pearce et al., 2014; Firth et al., 2015).

The ecological importance of sabellariid bio-constructions is widely acknowledged and is primarily due to their modulation of crucial abiotic and biotic processes, including substrate stabilization, sediment trapping and the provision of structurally complex microhabitats used for refuge, nursery and feeding by associated, mainly macrofaunal, organisms (Holt et al., 1998; Dubois et al., 2002, 2006; Cocito, 2004; Plicanti et al., 2017). Sabellariid reef-associated organisms span a wide range of taxa, although the largest proportion is typically represented by other polychaetes (Dias and Paula, 2001; Dubois et al., 2006; Cole and Chapman, 2007). The majority of species are common in other benthic habitats, but species using sabellariid reefs as their exclusive or preferential habitat are also known (Killeen and Light, 2000; Schimmenti et al., 2016) and contribute to make the *Sabellaria*-associated macrofauna generally more diverse and abundant than that of surrounding areas (Desroy et al., 2011). This macrofauna is also peculiar as it is represented, in the same habitat, by species typically found on hard, muddy or sandy bottom (Dubois et al., 2002).

Sabellaria reefs, however, represent highly dynamic systems exposed to several threats, including natural perturbations and increasing disturbance directly and/or indirectly related to human activities, which can affect both the habitat-forming species and their associated organisms. For instance, activities such as oyster farming and fishing may cause critical damage to the structure of both mature and developing reefs (Dubois et al., 2002, 2006, 2007). Even the physical disturbance produced by low intensities of trampling was experimentally indicated as responsible for significant reductions in the cover of intact *S. alveolata* concretions (Plicanti et al., 2016). Concomitantly, biogenic reefs are subject to physical damage by meteorological events like extreme storms, precipitation, temperature and acidification. The intensity, frequency and variance of such events was demonstrated by empirical data to increase in the last decades (e.g. Muller and Stone, 2001; Wolff et al., 2016) and is modelled to further increase in the near future due to climate change (Webster et al., 2005; Sriver and Huber, 2006; Trapp et al., 2007). The tube-building activity of *Sabellaria* may effectively repair small damaged areas of the reef within weeks or months (Cunningham et al., 1984; Vorberg, 2000; Plicanti et al., 2016), but heavier impacts may take years up to decades (Firth et al., 2015) to recover depending on temporally variable processes, such as larval supply (Gruet, 1986; Ayata et al., 2009). Permanent changes to the structure of the reef are also reported (Gibb et al., 2014).

The functional role played and the diversity and severity of threats they are subject to render sabellariid reefs a very valuable and vulnerable marine habitat, that must be considered for protection by European Union (EU) legislation, including the Habitats Directive (Directive 92/43/EEC), the Water Framework Directive (Directive 2000/60/EC) and the Marine Strategy Framework Directive (Directive 2008/56/EC). Moreover, *Sabellaria* reefs are included in the European Red List of Habitats (Gubbay et al., 2016) that is intended to provide an overview of the type, extent and status of benthic marine habitats across Europe. Unfortunately, these reefs, especially in the Mediterranean Sea, are listed as ‘Data Deficient’, thus needing comprehensive and specific investigation. In particular, *Sabellaria* reefs along the Italian coast are reported to cover thousands km^2 (IUCN, 2016), but largely lack empirical and quantitative data. Previous studies in the Mediterranean region focused on very local scales and a few morphological and ecological traits (Porras et al., 1996; La Porta and Nicoletti, 2009; Lezzi et al., 2015; Schimmenti et al., 2016), providing insufficient and fragmentary information to identify the current status, distribution, dynamics and threats of *Sabellaria* reefs. Such information, instead, is essential to assess their conservation needs and to guide effective management and protection strategies. This is especially true for the urgently needed knowledge on patterns of distribution of reefs and their associated biodiversity (but see Cole and Chapman, 2007). In fact, identifying the relevant scales of variation of organisms is an essential requirement to design protection schemes able to preserve not only those populations directly, but also their driving processes (García-Charton et al., 2000; Benedetti-Cecchi et al., 2003; Fraschetti et al., 2005a; Micheli et al., 2005; Bertocci et al., 2012; Anderson et al., 2014).

The present study was aimed at contributing to fill the above illustrated gaps by estimating and comparing spatial patterns of distribution, abundance and diversity of sabellariid bio-constructors and their associated fauna from biogenic reefs occurring in the shallow subtidal environment along the Italian coast of the Sicily Channel (central Mediterranean Sea). Specifically, we tested the hypothesis that patterns of the abundance, size and spatial variance of reef-forming polychaetes (*S. alveolata* and *S. spinulosa*), of the overall structure (identity and relative abundance of constituting taxa), richness and Shannon's diversity index of the associated faunal assemblage, and of the abundance and variance of the main faunal taxa differed at each of three scales ranging from tens of centimetres to ~200 km.

2. Methods

2.1. Study system

The Sicily Channel lies between the southern coast of Sicily (Italy) and the north-eastern coast of Tunisia, separating the Western from the Eastern Mediterranean sub-basins. As such, it is directly affected by the Atlantic Ionian Stream, which flows eastwards from the Atlantic Ocean through the Strait of Gibraltar (Poulain and Zambianchi, 2007). The main oceanographic conditions, coastal morphology and prevailing habitats in the study region are described in detail elsewhere (Schimmenti et al., 2016). Briefly, the present study was carried out at three locations (Triscina = TRI: 37°58' N, 12°80'E; Eraclea Minoa = ERA: 37°39' N, 13°28' E; Donnalucata = DON: 36°75' N, 14°64' E) distributed along about 190 km of coast in southern Sicily, which is characterized by a prevailing sandy bottom interspersed with meadows of the seagrass *Posidonia oceanica*, rocky shores and sabellariid reefs. A map of the study area illustrating the sampling locations is given in Appendix A.

The sampled reefs had a pillow-like form with a brain-like structure, ranging between 0.5 and 2 m in diameter and between 0.3 and 1.5 m in height and occurred between 1.5 and 3 m in depth depending on the location. All reefs occurred on a sandy bottom, interspersed with pebbles and close to a *P. oceanica* meadow at Triscina, and located at the base of a rocky breakwater at Donnalucata (for further details, see Schimmenti et al., 2016).

2.2. Sampling design and collection of data

Data were collected, by SCUBA divers, in June 2013 at two sabellariid reefs (hundreds of metres apart, hereafter indicated as sites) chosen at random in each location. Within each site, four replicate blocks (0.1 x 0.1 x 0.1 m, some metres apart) were collected at random using a hammer and a putty knife and immediately preserved, in separate bags, in 70% ethanol for subsequent analysis in the laboratory. In order to avoid edge effects due to the occurrence of different habitats adjacent to the sampled reefs at each location, all blocks were collected from the centre of each reef.

In the laboratory, all individuals of each *Sabellaria* species and of the associated fauna were sorted under a stereomicroscope, identified to the finest possible taxonomic level (species in most cases) and counted.

Moreover, the opercular length (maximum width of the operculum), considered as a proxy of body size and, hence, of the home-tube size, was measured on 40 *S. alveolata* (the dominant habitat-forming polychatete) individuals selected at random among those found in each of two replicate blocks chosen at random among the four available in each site and location.

2.3. Analysis of data

A two- way permutational multivariate analysis of variance (PERMANOVA: Anderson, 2001) based on Bray-Curtis untransformed dissimilarities was used to examine differences in the structure of the faunal assemblages associated with the *Sabellaria* habitat-forming polychaetes among locations and between sites. The model for the analysis included the factors ‘Location’ (random, three levels) and ‘Site’ (random, two levels, nested within Location), with four replicates provided by the blocks collected in each site. Since Bray-Curtis dissimilarities combine differences in both the identity and the relative abundance of taxa, the same analysis was repeated using either the matrix of raw abundances, or that of presence/absence data as input.

Multivariate patterns were visually displayed using Principal Component Ordination (PCO) based on Bray-Curtis dissimilarities calculated on both the abundance and the presence/absence data matrix. The SIMPER procedure (Clarke, 1993) was adopted to quantify the absolute (δ_i) and the percent (δ_i %) contribution of each taxon to the total dissimilarity between paired locations, using a cut-off of 75% of cumulative dissimilarity for excluding low contributions. Data on the abundance (number of individuals) of each *Sabellaria* species, their sum, the total number and the Shannon's diversity index (Shannon, 1948) of associated taxa, and the abundance of each taxon identified as relevant by SIMPER were analysed with analysis of variance (ANOVA) based on the same design as that used for PERMANOVA.

The opercular length of *S. alveolata* was analysed with a three-way ANOVA model including the same two factors of the previously described analyses, plus a third factor 'Replicate' (random, two levels represented by two replicate blocks in each site). The 40 individuals selected in each replicate block provided the replicates for this analysis.

Before each ANOVA, the assumption of homogeneity of variances was assessed with Cochran's *C* test, and data were log-transformed when the assumption was not met. When heterogeneous variances could not be stabilised by transformation, untransformed data were analysed and results were considered robust if not significant ($p>0.05$) or significant at $p<0.01$. These options were considered appropriate since the probability of Type II error is not affected by heterogeneous variances, and to compensate for increased probability of Type I error, respectively (Underwood, 1997).

Univariate variance components and their multivariate analogous at each scale were calculated, respectively, from ANOVA and PERMANOVA by equating empirical and expected mean squares (Winer et al., 1991; Underwood, 1997). Negative estimates of variance were interpreted as sample underestimates of very small to null variances and set to zero (Searle et al., 1992; Underwood, 1997). All variance components were calculated from untransformed data (e.g. Terlizzi et al., 2005).

3. Results

3.1. Habitat-forming species, richness and structure of associated faunal assemblages

Sabellaria alveolata and *S. spinulosa* coexisted in the sampled reefs, but the first species represented about 99% of all habitat-forming polychaetes and thus drove the overall patterns of abundance of total *Sabellaria* specimens counted throughout the study (Fig. 1 A-C). The abundance of the two *Sabellaria* species together and that of *S. alveolata* showed large and significant variation between sites, but not among locations (Table 1 and Table 2). Both species, however, differed in abundance between sites at Triscina more than at Eraclea Minoa and Donnalucata, with the first location showing a non-significant trend of larger abundances compared to the other two locations (Fig. 1 A and B). The range of *S. alveolata* opercular length was between 0.5 and 5 mm, with a mean (±1 SE) of 2.04 (±0.04) mm calculated over all sampled individuals ($n = 480$). Significant variation in this variable was found only between replicate blocks, although more than 83% of the total variance was provided by the among-individuals scale (Table 1 and Table 2 in Appendix B). In spite of graphically evident differences between sites within each location, the abundance of *S. spinulosa* also did not vary significantly, neither between sites nor among locations (Table 1 and Fig. 1 C), showing most variation at the among-replicates scale (Table 2).

In total, 86 faunal taxa (*Sabellaria* spp. excluded) associated with biogenic reefs, including 43 Annelida, 42 Arthropoda (27 Amphipoda and 14 Decapoda among Crustacea, and 1 Arachnida) and 1 Echinodermata (Ophiuroidea), were identified in this study (Appendix C) and used to calculate the total richness of taxa (a proxy for species richness) and in the multivariate analysis. Most taxa ($n=67$) were identified to species level, while the remaining 19 were identified to genus (n=12), family (n=5) or higher taxa (n=2). The total number of taxa was comparable across sites and locations (Table 1 and Fig. 1 D), with about 98% of the total variance provided almost equally by the replicate and the location scale (Table 2). The Shannon's diversity index varied significantly among locations, with a decreasing trend from Triscina to Donnalucata to Eraclea Minoa (Table 1 and Fig. 1 E) and most variance provided by the location scale (Table 2).

The structure of the reef-associated assemblages varied at each examined scale independently of analysing abundance or presence/absence data (Table 3). In both cases, most multivariate variation occurred at the among-replicates scale, followed by the among-locations and the between-sites scales (Table 2). The PCO clearly separated the three locations and the two sites within each location in terms of dissimilarities calculated from both abundance and presence/absence data (Fig. 2 A and B).

3.2. Faunal taxa associated with sabellarid reefs

The SIMPER procedure identified 11, 13 and 7 taxa as collectively contributing with over 75% to the total dissimilarity of Triscina *vs.* Eracla Minoa, Triscina *vs.* Donnalucata, and Eraclea Minoa *vs.* Donnalucata, respectively (Table 1 in Appendix D). Out of the total 17 taxa identified as either exclusive of one of the three contrasts or shared by multiple contrasts, all but Sipunculidae were analysed individually.

Significant differences among locations were found for 8 species, namely the polychaetes *Eulalia ornata*, *Syllis pulvinata*, *Syllis garciai*, *Nereis splendida* and *Arabella iricolor*, and the amphipods *Apolochus neapolitanus*, *Tethylembos viguieri* and *Caprella acanthifera* (Tables 1-3 in Appendix E). *Eulalia ornata* was, on average, the most abundant species and was commonly found at all sites and locations, although in higher numbers at Eraclea Minoa than at both Triscina and Donnalucata (Fig. 3 A). Differently, *S. pulvinata* (Fig. 3 B), *N. splendida* (Fig. 3 E), *A. iricolor* (Fig. 3 H), *A. neapolitanus* (Fig. 4 E) and *C. acanthifera* (Fig. 4H) were relatively more abundant at Donnalucata and very rare, if not completely absent (i.e., *A. iricolor* and *C. acanthifera* at Eraclea Minoa), at the other locations. All these species tended to vary in abundance also between sites, but significant differences at such scale were found for *S. pulvinata* only (Table 1 in Appendix E and Fig. 3 B). *Syllis garciai* (Fig. 3 I) and *T. viguieri* (Fig. 4 G), instead, were mostly found at Triscina, less abundant at Donnalucata and absent at Eraclea Minoa.

Adding to *S. pulvinata*, four more species showed significant variation between sites (Tables 1-3 in Appendix E), including the polychaetes *Syllis armillaris* (Fig. 3 C), *Syllis gracilis* (Fig. 3 D) and *Nereis rava* (Fig. 3 G), and the amphipod *Gammaropsis ulrici* (Fig. 4 B). In some cases, however, between-sites variability might have masked some visually evident differences among locations, such as in *S. armillaris* and *G. ulrici*, which tended to be relatively more abundant at Triscina, and in *S. gracilis*, which was represented in higher numbers at Eraclea Minoa (Fig. 3 C, Fig. 4 B and Fig. 3 D, respectively).

Four taxa did not show significant results (Tables 1-3 in Appendix E), including the polychaete *Brania arminii* (Fig. 3 F) and the amphipods *Jassa ocia* (Fig. 4 C), *Caprella rapax* (Fig. 4 D) and *Quadrimaera* sp. (Fig. 4 F). All of them were generally represented by low numbers, with *B. arminii* and *C. rapax* being absent at Eraclea Minoa, and *Quadrimaera* sp. being absent at Donnalucata (Fig. 3 F, Fig. 4 D and Fig. 4 F, respectively).

Sipunculidae were only present at Triscina and were not analysed statistically (Fig. 4 A).

Finally, the comparison of variance components of *Sabellaria*-associated taxa analysed individually indicated the smallest examined scale, i.e. among-replicates, as that providing the largest contribution in the majority (56%) of cases. These included, *N. splendida*, *B. arminii*, *A. iricolor*, *J. ocia*, *C. rapax*, *A. neapolitanus*, *Quadrimaera* sp., *T. viguieri* and *C. acanthifera* (Table 2). Only four (25%, represented by *S. armillaris*, *S. gracilis*, *N. rava* and *G. ulrici*) and three (19%, represented by *E. ornata*, *S. pulvinata* and *S. garciai*) species showed the largest variance at the site and the location scale, respectively (Table 2).

4. Discussion

This study tested the main hypothesis that patterns of distribution of habitat-forming sabellariid polychaetes (the dominant *S. alveolata* and the much less numerous *S. spinulosa*) and of the overall structure and individual abundance of associated fauna in the Sicily Channel varied at spatial scales ranging from metres (among replicates) to ~50-100 km (among locations). Results indicated that relevant scales of variation were not consistent across all examined organisms. While the abundance of total *Sabellaria* and of the dominant *S. alveolata* varied significantly at the site, but not the location, scale, the structure of the associated assemblages and the abundance of many of the most common taxa showed marked differences at the largest scale. This observation is rather surprising since it could be expected that the patterns of distribution of bio-constructors are matched by those of the faunal taxa using biogenic reefs as habitat. Moreover, obvious macroscopic differences in the general reef structure, size, surrounding habitats and depth among sampled locations (as illustrated in detail by Schimmenti et al., 2016) did not correspond to significant differences in patterns of distribution and abundance of sabellariid worms at the same scale. The present findings suggest that the structure of the habitat and the surrounding environment, although not quantified in this study, may actually shape the structure and distribution of associated assemblages, but that this effect can be decoupled from the mere abundance of the habitat-forming species. An analogous observation was made by Schlund et al. (2016), who reported that different structures (platforms *vs.* ‘reefs’, i.e., more massive formations) of *S. alveolata* bio-constructions in the Bay of Mont-Saint-Michel were characterized by different macrofaunal assemblages, yet comparable density of *S. alveolata*. Such differences are often explained with critical changes in the structural complexity of the bio-construction, which would provide different ranges, types and extent of microhabitats to diverse organisms (Gruet, 1986; Porras et al., 1996; Dubois et al., 2002). All present reefs, however, were characterized by a comparable convoluted tridimensional structure (detailed pictures are shown in Schimmenti et al., 2016), suggesting that such mechanisms were relatively less important in the studied system.

Local environmental conditions, instead, may be more relevant for determining location-scale differences in the structure, diversity and abundance of the reef-associated fauna. A main driving factor could involve the colonization of different organisms from surrounding habitats (Dubois et al., 2006). All the sampled locations, in particular, presented sabellariid reefs interspersed within a predominant sandy bottom, but these were close to a *P. oceanica* meadow at Triscina and to a breakwater rocky barrier at Donnalucata, i.e., markedly different habitats that are likely to provide different pools of colonizers to adjacent *Sabellaria*-associated assemblages. For example, shallow hard substrates in the Mediterranean Sea are reported to host diverse and abundant assemblages of syllid polychaetes (Chatzigeorgiou et al., 2012; Musco, 2012; Dorgham et al., 2014), a feature that could have contributed to the larger abundance of *S. pulvinata*, the most numerous syllid in this study, at Donnalucata compared to Triscina. Concomitantly, significant among-locations variation in the distribution of reef-associated fauna could also be driven by patterns of dispersal of organisms varying over the same scale (e.g., Johnson et al., 2001; Fraschetti et al., 2005b). This explanation is made plausible by the potential effect of the Atlantic Ionian Stream originating from the Atlantic Ocean, entering the Mediterranean Sea through the Strait of Gibraltar and reaching the surface of the Sicily Channel in its eastward path. Such an oceanographic feature is associated with environmental heterogeneity in terms of salinity, temperature (Lermusiaux and Robinson, 2001) and productivity (Ciappa, 2009) along the southern coast of Sicily. In addition, transportation through the Atlantic Ionian Stream is likely to produce a gradient of distribution of drifting colonizers which could have resulted in the observed variation among locations tens-100 km apart along about 200 km of coast. On the contrary, other factors potentially relevant for directly and indirectly driving differences in reef-associated assemblages, such as the tidal height and wave exposure (e.g. Schlund et al., 2016, and references therein), were less likely in the present system given the comparable depth and exposure to south-western winds of all sampled reefs.

The peculiar position of the Sicily Channel at the separation between the Western and the Eastern Mediterranean sub-basins may also be responsible for the local coexistence of two *Sabellaria* species, although with a clear dominance of *S. alveolata*. So far, the studies available for the Mediterranean Sea suggested that only *S. alveolata* and only *S. spinulosa* build-up reefs in the Western and the Eastern (Adriatic Sea included) sub-basins, respectively (La Porta and Nicoletti, 2009; Lezzi et al., 2015; Gubbay et al., 2016). Moreover, the present locations are the southernmost records of the overall distribution of *S. alveolata* and *S. spinulosa* reefs. Upwelling events occurring along the southern coast of Sicily (e.g. Piccioni et al., 1988) may be responsible, at least in part, for such biogeographic patterns. In non-Mediterranean regions, the majority of studies reported the exclusive occurrence of *S. alveolata* (e.g., Wilson, 1976; Dubois et al., 2002; Plicanti et al., 2016) or *S. spinulosa* (e.g., Hendrick and Foster-Smith, 2006), with the first species normally being more common and abundant in the intertidal environment (e.g., Firth et al., 2015), while the second in the subtidal environment (e.g., Pearce et al., 2014). In some cases, coexisting *S. alveolata* and *S. spinulosa* have been recorded (e.g., Wilson, 1970a, 1970b), but not at the small scale documented in the Sicily Channel.

Despite specific patterns of significant or non-significant differences at each examined scale, the structure of the reef-associated assemblages and the abundance of the majority of their constituting species showed the highest variance at the smallest (i.e., among replicates) scale. Recurrent analogous findings suggest that relevant variation at spatial scales of tens-hundreds of centimetres up to tens-hundreds of metres is a common feature of a wide range of benthic organisms, habitats and geographic areas (Underwood and Chapman, 1996; Kendall and Widdicombe, 1999; Benedetti-Cecchi, 2001; Fraschetti et al., 2005b; Terlizzi et al., 2007;

Bertocci et al. 2012), often explained primarily with the effects of the topography of the substratum (e.g. Denny et al., 2004). In sabellariid reefs, small-scale heterogeneity could be due to the availability of different microhabitats formed by worms, hence tubes, of a range of sizes. The present data did not show significant differences in the opercular size of *S. alveolata*; nevertheless, most variance in this trait occurred at small scales (among individuals within the same block and between replicate blocks), suggesting that the heterogeneous spatial pattern of available microhabitats could have maintained an analogously heterogeneous distribution of the associated fauna. However, a previous comparison of patterns of distribution of annelids associated with *S. alveolata* reefs from Wales and Portugal indicated that the identification of small-scale variability can also depend on the level of taxonomic resolution, being less likely for fine taxonomic groups, such as species and families, and more evident for broad taxonomic groups, such as classes and phyla (Cole and Chapman, 2007). Instead, other processes operating at a larger scale (hundreds of metres, i.e., between sites) may be invoked to explain the large variance of *S. alveolata*. For instance, a potentially relevant factor which could vary at this scale is the grain size of the sand used by the worms to build the tubes. Changes in this variable between reefs separated by a distance comparable with that of present sites were reported in Wales (UK) and related with changes in growth, morphology and composition of *S. alveolata* aggregations (Naylor and Viles, 2000). Indeed, the degree of development or degradation of sabellariid reefs is typically associated with considerable changes in their hosted biodiversity, with the taxonomic richness of associated benthic macrofauna tending to decrease within ‘healthy’ areas with large densities of honeycomb worms, and to decrease in degraded areas (Gruet and Bodeur, 1997), often characterized by an intense colonization by epibionts (Dubois et al., 2006). Quantitative data on the healthy *vs.* degraded status of our sampled reefs were not available, but some considerations may lead to exclude such differences as the most likely explanation for between-sites variation. In fact, the reefs sampled at each location were all characterized by the virtual lack of conspicuous epibionts (detailed pictures are reported by Schimmenti et al., 2016). At the same time, no significant differences between sites were found for the opercular length of *S. alveolata*. Assuming that the proportion of small *S. alveolata* individuals, being directly related with the number of young recruits, should differ depending on the development stage, and possibly the level of degradation, of reefs, it could be hypothesized that the sampled reefs were comparable in terms of such variables.

Within the fauna associated with present biogenic reefs, the most abundant species was *E. ornata*. This phyllodocid polychaete uses *S. alveolata* bio-constructions as a preferential habitat, as reported along European east Atlantic and Mediterranean coasts (Pleijel and Dales, 1991; Schimmenti et al., 2016). Actually, the Atlantic-Mediterranean distribution of *E. ornata* mirrors that of *S. alveolata* reefs, suggesting the fidelity of the phyllodocid to such biogenic habitat (Schimmenti et al., 2016). Finding *E. ornata* as the most abundant species in *S. alveolata* reefs opens ecologically relevant questions, including whether Mediterranean *Eulalia* specimens previously named as *E. clavigera* or *E. viridis* were correctly identified, and what functional role *E. ornata* plays in the functioning and dynamics of biogenic reefs. If carnivorous like most phyllodocids, such as *E. viridis* (Jumars et al., 2015), large numbers of *E. ornata* should rely on the availability of abundant prey in the reef. Since most biomass in this system is provided by the bio-constructing worm itself, intense predation by *E. ornata* on *S. alveolata* could critically affect the structure and dynamics of the entire reef (Schimmenti et al., 2016).

Following *E. ornata*, the syllid *S. pulvinata* was common and numerous in the examined samples, providing interesting data on its occurrence in the Mediterranean Sea. Specifically, *S. pulvinata* was not listed in the Italian fauna (Castelli et al., 1995) until recently (Musco et al., 2004), possibly due to synonymy (Licher, 1999). Concomitantly, the peculiarity of the faunal assemblages of sabellariid reefs in the Sicily Channel is reinforced by the occurrence of some numerically scarce species, such as the amphipods *G. ulrici* and *J. ocia*. The former species is considered endemic to the Mediterranean Sea, but records along the Italian coasts are very sparse and rare (but see Lo Brutto and Sparla, 1993; Bedini et al., 2011; Iaciofano et al., 2015). The latter was previously found in large abundances within *S. alveolata* reefs located along the central Tyrrhenian coast, about 500 km north of present locations (La Porta et al., 2009), and, therefore, could be a species using the sabellariid bio-constructions as a preferential habitat.

In conclusion, identifying and testing the discussed processes as responsible for patterns of distribution, abundance and diversity of sabellariid reefs and associated fauna were beyond the goals of this study. Being based on a descriptive approach, present findings contribute to propose plausible drivers of such patterns, but future, specifically designed, experiments are needed to elucidate the actual causal role of each process and of their possible interactions. Nevertheless, if including biogenic reefs in European directives and in the Red List of endangered habitats has an obvious goal in protecting them as ecologically important, but threatened, systems, the present findings have several implications for establishing the corresponding priorities. First, identifying the relevant scales of variation of habitat-forming species and of their associated biodiversity, as well as their faunal peculiarities, is crucial to design protection schemes suitable to guarantee a representative set of target populations and assemblages and, likely, of the processes driving their spatial variation. To this end, effective strategies of protection of sabellariid reefs in the Sicily Channel would require to include all locations examined here as collectively providing a representative sample of the biota associated with this habitat. Any future decision in this direction, however, will need to be based on the confirmation of present patterns through temporally replicated studies. Indeed, the present findings necessarily apply only to the particular time at which this study was carried out, and it cannot be assumed that spatial patterns are consistent over time (e.g. Underwood and Petraitis, 1993; Benedetti-Cecchi et al., 2001). Second, recent experimental and theoretical investigations started to clarify how natural and anthropogenic perturbations, especially those due to climate change, ultimately modulate morphological, physiological and distributional responses of natural populations and assemblages and the ecosystem services they provide (reviewed by Torossian et al., 2016). In this context, this study may provide reference data useful to relate climatic variation with ongoing changes in patterns of an important biogenic habitat and its supporting species at the edge of their distribution limits. Marginal populations are assumed to deal with sub-optimal environmental conditions (Bridle and Vines, 2007) which could reduce their ability to resist to and/or recover from further disturbances (Guo et al., 2005; Hampe and Petit, 2005). In addition, they are, like in the present case, often characterized by distinctive ecological characteristics that need to be preserved against the negative impact of environmental modifications, such as those observed and predicted as a consequence of climate change, especially in the Mediterranean Sea (e.g. Marbà et al., 2015). Finally, sabellariid reefs are the focus of recent attempts to restore their habitats where degraded (e.g. Callaway et al., 2014), as required by the Habitats Directive. Present information on ecological and biological patterns of sabellariid reefs in the Sicily Channel may contribute to assess their status, establish terms of comparison for similar reefs elsewhere and evaluate the effectiveness of possible restoration interventions of this habitat and its hosted biota.

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References

Achary, G.P.K., 1974. Polychaete of the family Sabellariidae with special reference to their intertidal habitat. Proceedings of the Indian Natural Science Academy 38, 442-455.

Anderson, A.B., Bonaldo, R.M., Barneche, D.R., Hackradt, C.W., Félix-Hackradt, F.C., García-Charton, J.A., Floeter, S.R., 2014. Recovery of grouper assemblages indicates effectiveness of a marine protected area in Brazil. Marine Ecology Progress Series 514, 207-215.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32-46.

Ayata, S.D., Ellien, C., Dumas, F., Dubois, S., Thiébaut, E., 2009. Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata*: role of hydroclimatic processes on the sustainability of biogenic reefs. Continental Shelf Research 29, 1605-1623.

Bedini, R., Pertusati, M., Batistini, F., Piazzi, L., 2011. Spatial and temporal variation of motile macro-invertebrate assemblages associated with *Posidonia oceanica* meadows. Acta Adriatica 52, 201-214.

Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W. and Webster, N.S., 2013. Could some coral reefs become sponge reefs as our climate changes? Global Change Biology 19, 2613-2624.

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Marine Ecology Progress Series 215, 79-92.

Benedetti-Cecchi, L., Bulleri, F., Acunto, S., Cinelli, F., 2001. Scales of variation in the effects of limpets on rocky shores in the northwest Mediterranean. Marine Ecology Progress Series 209, 131-141.

Benedetti-Cecchi, L., Bertocci, I., Micheli, F., Maggi, E., Fosella, T., Vaselli, S., 2003. Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the Northwest Mediterranean. Marine Environmental Research 55, 429-458.

Bertocci, I., Dominguez, R., Freitas, C., Sousa-Pinto, I., 2012. Patterns of variation of intertidal species of commercial interest in the Parque Litoral Norte (North Portugal) MPA: comparison with three reference shores. Marine Environmental Research 77, 60-70.

Bridle, J.R., Vines, T.H., 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends in Ecology and Evolution 22, 140-147.

Callaway, R., Lock, J., Bishop, E., Blazey, T., 2014. A tidal energy lagoon in Swansea Bay: Optimising its value for biodiversity by creating an artificial reef. Proceedings of the 2nd International Conference on Environmental Interactions of Marine Renewable Energy Technologies (EIMR2014), Stornoway, Isle of Lewis, UK.

Castelli, A., Abbiati, M., Badalamenti, F., Bianchi, C.N., Cantone, G., Gambi, M.C., Giangrande, A., Gravina, M.F., Lanera, P., Lardicci, C., Somaschini, A., Sordino, P., 1995. Annelida Polychaeta, Pogonophora, Echiura, Sipuncula, in: Minelli, A., Ruffo, S., La Posta, S. (Eds.), Checklist delle specie della fauna italiana, Calderini, Bologna, Vol. 19, pp. 1-45.

Chatzigeorgiou, G., Faulwetter, S., López, E., Sardá, R., Arvanitidis, C., 2012. Can coastal biodiversity measured in four Mediterranean sites be representative of the region? A test for the robustness of the NaGISA protocol by using the hard substrate syllid (Annelida, Polychaeta) taxo-communities as a surrogate. Hydrobiologia 691, 147-156.

Ciappa, A.C., 2009. Surface circulation patterns in the Sicily Channel and Ionian Sea as revealed by MODIS chlorophyll images from 2003 to 2007. Continental Shelf Research 29, 2099-2109.

Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117-143.

Cocito, S., 2004. Bioconstruction and biodiversity: their mutual influence. Scientia Marina 68, 137-144.

Cole, V.J., Chapman, M.G., 2007. Patterns of distribution of annelids: taxonomic and spatial inconsistencies between two biogeographic provinces and across multiple spatial scales. Marine Ecology Progress Series 346, 235-241.

Council Directive 92/43/EEC. The Habitats Directive, http://eur-lex.europa. eu/legal-content/EN/TXT/?uri=CELEX:31992L0043. Last accessed 12 May 2017.

Cunningham, P.N., Hawkins, S.J., Jones, H.D., Burrows, M.T., 1984. The biogeography and ecology of *Sabellaria alveolata*. Nature Conservancy Council CSD Report No. 535, Peterborough, UK.

Denny, M.W., Helmuth, B., Leonard, G.H., Harley, C.D.G., Hunt, L.J.H., Nelson, E.K., 2004. Quantifying scale in ecology: lessons from a wave-swept shore. Ecological Monographs 73, 513-532.

Desroy, N., Dubois, S.F., Fournier, J., Ricquiers, I., Le Mao, P., Guerine, L., Gerla, D., Rougerie, M., Legendre, A., 2011. The conservation status of *Sabellaria alveolata* (L.) (Polychaeta: Sabellariidae) reefs in the Bay of Mont Saint Michel. Aquatic Conservation: Marine and Freshwater Ecosystems 21, 462-471.

Dias, A.S., Paula, J., 2001. Associated fauna of *Sabellaria alveolata* colonies on the central coast of Portugal. Journal of the Marine Biological Association of the United Kingdom 80, 169-170.

Directive 2000/60/EC. The EU Water Framework Directive, http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32000L0060. Last accessed 12 May 2017.

Directive 2008/56/EC. The Marine Strategy Framework Directive, http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32008L0056. Last accessed 12 May 2017.

Dorgham, M.M., Hamdy, R., El Rashidy, H.H., Atta, M.M., Musco, L., 2014. Distribution patterns of shallow water polychaetes (Annelida) along the Alexandria coast, Egypt (eastern Mediterranean). Mediterranean Marine Science 15, 635-649.

Dubois, S., Retière, C., Olivier, F., 2002. Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs: effects of human disturbances. Journal of the Marine Biological Association of the United Kingdom 82, 817-826.

Dubois, S., Commito, J.A., Olivier, F., Retière, C., 2006. Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. Estuarine, Coastal and Shelf Science 68, 635-646.

Dubois, S., Comtet, T., Retière, C., Thiébaut, E., 2007. Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel, France. Marine Ecology Progress Series 346, 243-254.

European Commission DG Environment, 2003. Interpretation Manual of European Union Habitats. EUR15/2.

Firth, L.B., Mieszkowska, N., Grant, L.M., Bush, L.E., Davies, A.J., Frost, M.T., Moschella, P.S., Burrows, M.T., Cunningham, P.N., Dye, S.R., Hawkins, S.J., 2015. Historical comparisons reveal multiple drivers of decadal change of an eco system engineer at the range edge. Ecology and Evolution 5, 3210-3222.

Fraschetti, S., Terlizzi, A., Bussotti, S., Guarnieri, G., D'Ambrosio, P., Boero, F., 2005a. Conservation of Mediterranean seascapes: analyses of existing protection schemes. Marine Environmental Research 59, 309-332.

Fraschetti, S., Terlizzi, A., Benedetti-Cecchi, L., 2005b. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. Marine Ecology Progress Series 296, 13-29.

García-Charton, J.A., Williams, I., Pérez-Ruzafa, A., Milazzo, M., Chemello, R., Marcos, C., Kitsos, M.-S., Koukouras, A., Riggio, S., 2000. Evaluating the ecological effects of Mediterranean marine reserves: habitat, scale and the natural variability of ecosystems. Environmental Conservation 27, 159-178.

Gibb, N., Tillin, H., Pearce, B., Tyler-Walters, H., 2014. Assessing the sensitivity of Sabellaria spinulosa reef biotopes to pressures associated with marine activities. JNCC Report No. 504, Peterborough, UK.

Gruet, Y., 1986. Spatiotemporal changes of sabellarian reefs built by the sedentary polychaete *Sabellaria alveolata* (Linné). Marine Ecology 7, 303-319.

Gruet, Y., Bodeur, Y., 1997. Les récifs d'Hermelles, in: Dauvin, J.-C. (Ed.), Les biocénoses marines et littorales françaises des côtes Atlantique, Manche et Mer du Nord, synthèse, menaces et perspectives. Collection Patrimoines naturels: Série Patrimoine ecologique, 28, Muséum National d'Histoire naturelle: Paris, pp. 168-176.

Gubbay, S, Sanders, N, Haynes, T., and 144 others, 2016. European Red List of Habitats. Part 1. Marine Habitats. Publications Office of the European Union, Luxembourg.

Guo, Q.F., Taper, M., Schoenberger, M., Brandle, J., 2005. Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108, 47-57.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79-90.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8, 461-467.

Hendrick, V.J., Foster-Smith, R.L., 2006. *Sabellaria spinulosa* reef: a scoring system for evaluation "reefiness" in the context of the Habitat Directive. Journal of the Marine Biological Association of the United Kingdom 86, 665-677.

Holt, T.J., Rees, E.I., Hawkins, S.J., Seed, R., 1998. Biogenic Reefs (Volume IX). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science (UK Marine SACs Project).

Iaciofano, D., Musco, l., Vega Fernández, T., Lo Brutto, S., 2015. Crostacei anfipodi associati a *reef* di *Sabellaria alveolata* (L.) (Annelida) dello Stretto di Sicilia (Mar Mediterraneo). Biologia Marina Mediterranea 22, 95-96.

IUCN (International Union for Conservation of Nature), 2016. The IUCN Red List of Threatened Species. Version 2016-3, http://www.iucnredlist.org. Last accessed 12 May 2017.

Johnson, M.P., Allcock, A.L., Pye, S.E., Chambers, S.J., Fitton, D.M., 2001. The effects of dispersal mode on the spatial distribution patterns of intertidal molluscs. Journal of Animal Ecology 70, 641-649.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373-386.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: An update of Polychaete feeding guilds. Annual Review of Marine Science 7, 497-520.

Kendall, M.A., Widdicombe, S., 1999. Small scale patterns in the structure of macrofaunal assemblages of shallow soft sediments. Journal of Experimental Marine Biology and Ecology 237, 127-140.

Killeen, I.J., Light, J.M., 2000. *Sabellaria*, a polychaete host for the grastropods *Noemiamea dolioliformis* and *Graphis albida*. Journal of the Marine Biological Association of the United Kingdom 80, 571-573.

La Porta, B., Nicoletti, L., 2009. *Sabellaria alveolata* (L.) reefs in the central Tyrrhenian Sea (Italy) and associated polychaete fauna. Zoosymposia 2, 527-536.

La Porta, B., Targusi, M., Lattanzi, L., La Valle, P., Nicoletti, L., 2009. Analisi della fauna associata alle biocostruzioni a *Sabellaria alveolata* (L.) in relazione al loro stato di conservazione. Biologia Marina Mediterranea 16, 36-38.

Lermusiaux, P.F.J., Robinson, A.R., 2001. Features of dominant mesoscale variability, circulation patterns and dynamics in the Strait of Sicily. Deep Sea Research Part I: Oceanographic Research Papers 48, 1953-1997.

Lezzi, M., Cardone, F., Mikac, B., Giangrande, A., 2015. Variation and ontogenetic changes of opercolare paleae in a population of *Sabellaria spinulosa* (Polychaeta: Sabellaridae) from the South Adriatic Sea, with remarks on larval development. Scientia Marina 79, 137-150.

Licher, F., 1999. Revision der Gattung *Typosyllis* Langherans, 1879 (Polychaeta: Syllidae). Morphologie, taxonomic und Phylogenic. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 551, 1-336.

Lo Brutto, S., Sparla, M.P., 1993. Anfipodi associati dei banchi di filtratori nel golfo di Castellammare (Sicilia N/W). Biologia Marina (Suppl. Notiziario SIBM) 1, 295-296.

Marbá, N., Jordá, G., Agustí, S., Girard, C., Duarte, C.M., 2015. Footprints of climate change on Mediterranean Sea biota. Frontiers in Marine Science 2, 00056.

Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, G.C., Romano, F., 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. Ecological Monographs 75, 81-102.

Muller, R.A., Stone, G.W., 2001. A climatology of tropical storm and hurricane strikes to enhance vulnerability prediction for the southeast U.S. coast. Journal of Coastal Research 17, 949-956.

Musco, L., 2012. Ecology and diversity of Mediterranean hard-bottom Syllidae (Annelida): a community-level approach. Marine Ecology Progress Series 461, 107-119.

Musco, L., Cavallo, A., Giangrande, A., 2004. I sillidi (Annelida, Polychaeta) del litorale brindisino: possibilità di un loro impiego come indicatori di qualità dell'ambiente. Thalassia Salentina 27, 161-174.

Naylor, L.A., Viles, H.A., 2000. A temperate reef builder: an evaluation of the growth, morphology and composition of *Sabellaria alveolata* (L.) colonies on carbonate platforms in South Wales, in: Insalaco, E.R., Skelton, P.W., Palmer, T.J. (Eds.), Carbonate platform systems: components and interactions. Special Publications, Geological Society, London, Vol. 178, pp. 9-19.

Pearce, B., Fariñas-Franco, J.M., Wilson, C., Pitts, J., deBurgh, A., Somerfield, P.J., 2014. Repeated mapping of reefs constructed by *Sabellaria spinulosa* Leuckart 1849 at an offshore wind farm site. Continental Shelf Research 83, 3-13.

Piccioni, A., Gabriele, M., Salusti, E., Zambianchi, E., 1988. Wind-induced upwellings off the southern coast of Sicily. Oceanologica Acta 11, 309-321.

Pleijel, F., Dales, R.P., 1991. Polychaetes: British Phyllodocoideans, Typhloscolecoideans and Tomopteroideans, in: Kermack, D.M., Barnes, R.S.K. (Eds.), Synopses of the British Fauna (New Series). Universal Book Services, Oegstgeest, Netherlands, Vol. 45.

Plicanti, A., Domínguez, R., Dubois, S.F., Bertocci I., 2016. Human impacts on biogenic habitats: effects of experimental trampling on *Sabellaria alveolata* reefs. Journal of Experimental Marine Biology and Ecology 478, 34-44.

Plicanti, A., Iaciofano, D., Bertocci, I., Lo Brutto, S., 2017. The Amphipod assemblages of *Sabellaria alveolata* reefs from the NW coast of Portugal: an account of the present knowledge, new records, and some biogeographic considerations. Marine Biodiversity 47, 521-534.

Porras, R., Bataller, J.V., Murgui, E., Torregrosa, M.T., 1996. Trophic structure and community composition of polychaetes inhabiting some *Sabellaria alveolata* (L.) reefs along the Valencia Gulf Coast, western Mediterranean. PSZNI Marine Ecology 17, 583-602.

Poulain, P.M., Zambianchi, E., 2007. Surface circulation in the central Mediterranean Sea as deduced from Lagrangian drifters in the 1990s. Continental Shelf Research 27, 981-1001.

Schimmenti, E., Musco, L., Lo Brutto, S., Mikac, B., Nygren, A., Badalamenti, F., 2016. Mediterranean record of *Eulalia ornata* (Annelida: Phyllodocida) corroborating its fidelity link with the *Sabellaria alveolata* reef habitat. Mediterranean Marine Science 17, 359-370.

Schlund, E., Basuyaux, O., Lecornu, B., Pezy, J.-P., Baffreau, A., Dauvin, J.-C., 2016. Macrofauna associated with temporary *Sabellaria alveolata* reefs on the west coast of Cotentin (France). SpringerPlus 5, 1260.

Searle, S.R., Casella, G., McCulloch, C.E., 1992. Variance components. John Wiley & Sons Inc., New York, USA.

Shannon, C.E., 1948. A mathematical theory of communication. The Bell System Technical Journal 27, 379-423.

Sheppard, C.R.C., Davy, S.K., Pilling, G.M., 2009. The biology of coral reefs. Oxford University Press, Oxford, UK.

Sriver, R., Huber, M., 2006. Low frequency variability in globally integrated tropical cyclone power dissipation. Geophysical Research Letters 33, L11705.

Terlizzi, A., Benedetti-Cecchi, L., Bevilacqua, S., Fraschetti, S., Guidetti, P., Anderson, M.J., 2005. Multivariate and univariate asymmetrical analyses in environmental impact assessments: a case study of Mediterranean subtidal sessile assemblages. Marine Ecology Progress Series 289, 27-42.

Terlizzi, A., Anderson, M.J., Fraschetti, S., Benedetti-Cecchi, L., 2007. Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. Marine Ecology Progress Series 332, 25-39.

Torossian, J.L., Kordas, R.L., Helmuth, B., 2016. Cross-scale approaches to forecasting biogeographic responses to climate change. Advances in Ecological Research 55, 371-433.

Trapp, R., Diffenbaugh, N.S., Brooks, H.E., Baldwin, M.E., Robinson, E.D., Pal, J.S., 2007. Changes in severe thunderstorm environment frequency during the 21st century caused by anthropogenically enhanced global radiative forcing. Proceedings of the National Academy of Sciences of the United States of America 104, 19719-19723.

Underwood, A.J., 1997. Experiments in Ecology: Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK.

Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107, 212-224.

Underwood, A.J., Petraitis, P.S., 1993. Structure of intertidal assemblages in different locations: how can local processes can be compared? In: Rickefs, R., Schluter, D. (Eds.), Species diversity in ecological communities. University of Chicago Press, Chicago, USA, pp. 38-51.

Vorberg, R., 2000. Effects of shrimp fisheries on reefs of *Sabellaria spinulosa* (Polychaeta). ICES Journal of Marine Science 57, 1416-1420.

Webster, P.J., Holland, G.J., Curry, J.A., Chang, H.R., 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science 309, 1844-1846.

Wilson, D.P., 1970a. The larvae of *Sabellaria spinulosa* and their settlement behaviour. Journal of the Marine Biological Association of the United Kingdom 50, 33-52.

Wilson, D.P., 1970b. Additional observations on larval growth and settlement of *Sabellaria alveolata*. Journal of the Marine Biological Association of the United Kingdom 50, 1-32.

Wilson, D.P., 1971. *Sabellaria* colonies at Duckpool, North Cornwall, 1961–1970. Journal of the Marine Biological Association of the United Kingdom 51, 509-580.

Wilson, D.P., 1976. *Sabellaria alveolata* (L.) at Duckpool, North Cornwall, 1975. Journal of the Marine Biological Association of the United Kingdom 56, 305-310.

Winer, B.J., Brown, D.R., Michelis, K.M., 1991. Statistical principles in experimental design. McGraw-Hill, New York, USA.

Wolff, N.H., Wong, A., Vitolo, R., Stolberg, K., Anthony, K.R.N., Mumby, P.J., 2016. Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. Coral Reefs 35, 613-623.

Wood, A.C.L., Probert, P.K., Rowden, A.A., Smith, A.M., 2012. Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 22, 547-563.

Table 1. Results of analysis of variance (ANOVA) on the abundance (number of individuals) of *Sabellaria* spp., the total richness (number) of taxa and the Shannon's diversity index (H) of assemblages associated with sabellarid reefs in the Sicily Channel. * p<0.05, ** p<0.01, *** p<0.001.

		***Sabellaria* total**		***Sabellaria alveolata***		***Sabellaria spinulosa***		**Richness**		**Shannon's H**		
Source of variation	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	Denominator
Location	2	1.43	0.79	1.41	0.77	2.88	1.34	215.54	8.07	1.80	10.51	Site(Location)
Site(Location)	3	1.80	40.70***	1.83	42.25***	2.15	1.45	26.71	1.19	0.17	1.36	Residual
Residual	18	0.04		0.04	1.49		22.43			0.13		
Cochran's test		*C* = 0.375		*C* = 0.374		*C* = 0.306		*C* = 0.518		*C* = 0.496		
Transformation		Ln(x+1)		Ln(x+1)		Ln(x+1)		None		None		

Table 2. Components of variation, expressed as untransformed variance values (σ^2) and percentage of total variance (%), at each of three spatial scales (among replicates, between sites and among locations) of the structure of whole faunal assemblages (*Sabellaria* spp. excluded), individual abundance of *Sabellaria* spp., richness (total number of taxa), Shannon's diversity index (H) and individual abundance of taxa associated with sabellarid reefs in the Sicily Channel.

	Replicate scale		**Site scale**		**Location scale**	
Variable	σ^2	%	σ^2	%	σ^2	%
Sabellaria tot.	104151	17.69	484621	82.31	0	0
Sabellaria alveolata	99452	17.15	480533	82.85	0	0
Sabellaria spinulosa	111.72	90.09	0	0	12.29	9.91
Richness	22.43	47.62	1.07	2.27	23.60	50.11
Shannon's H	0.13	38.24	0.01	2.94	0.20	58.82
Assemblage (abundances)	888.20	44.73	479.14	24.13	618.36	31.14
Assemblage (P/A)	1222.40	62.05	197.50	10.03	550.16	27.98
Eulalia ornata	521.94	44.32	130.70	11.12	522.95	44.48
Syllis pulvinata	368.22	29.40	144.53	11.54	739.62	59.06
Syllis armillaris	20.72	19.44	85.88	80.56	0	0
Syllis gracilis	14.18	29.67	25.17	52.67	8.44	17.66
Nereis splendida	67.63	79.79	0	0	17.13	20.21
Brania arminii	32.76	47.62	16.86	24.51	19.18	27.88
Nereis rava	1.17	37.86	1.92	62.14	0	0
Arabella iricolor	5.15	73.05	0	0	1.90	26.95
Syllis garciai	0.97	40.76	0	0	1.41	59.24
Gammaropsis ulrici	106.36	24.77	313.51	73.00	9.59	2.23

Jassa ocia	159.28	67.59	76.39	32.41	0	0
Caprella rapax	12.44	65.20	6.64	34.80	0	0
Apolochus neapolitanus	5.69	61.71	0	0	3.53	38.29
Quadrimaera sp.	6.81	92.15	0.31	4.19	0.27	3.65
Tethylembos viguieri	7.06	72.26	0	0	2.71	27.74
Caprella acanthifera	7.43	80.41	0	0	1.81	19.59

Table 3. Results of permutational multivariate analysis of variance (PERMANOVA) on the structure of sabellarid reef assemblages (*Sabellaria* spp. excluded), examined as abundance or presence/absence data, in the Sicily Channel. Significant effects are indicated in bold.

Source of variation	df	MS	pseudo-*F*	p	Unique perm.	Denominator
Abundance						
Location	2	7751.7	2.8	**0.016**	999	Site(Location)
Site(Location)	3	2804.8	3.2	**0.001**	998	Residual
Residual	18	888.2				
Presence/Absence						
Location	2	6413.5	3.2	**0.005**	998	Site(Location)
Site(Location)	3	2012.2	1.6	**0.014**	997	Residual
Residual	18	1222.4				

FIGURE CAPTIONS

Fig. 1. Mean (+SE, n = 4) abundance of total *Sabellaria*, *S. alveolata*, *S. spinulosa*, richness of taxa and Shannon's diversity index from three locations (TRI = Triscina, ERA = Eraclea Minoa, DON = Donnalucata) and two sites (paired bars of the same colour) within each location in the Sicily Channel.

Fig. 2. Principal Component Ordination (PCO) of assemblages (*Sabellaria* spp. excluded) from sabellarid reefs between three locations and two sites within each location in the Sicily Channel.

Fig. 3. Mean (+SE, n = 4) abundance of nine polychaete species associated with sabellarid reefs from three locations and two sites (paired bars of the same colour) within each location in the Sicily Channel. Abbreviations as in Fig. 2.

Fig. 4. Mean (+SE, n = 4) abundance of Sipunculidae and seven amphipod taxa associated with sabellarid reefs from three locations and two sites (paired bars of the same colour) within each location in the Sicily Channel. Abbreviations as in Fig. 2.

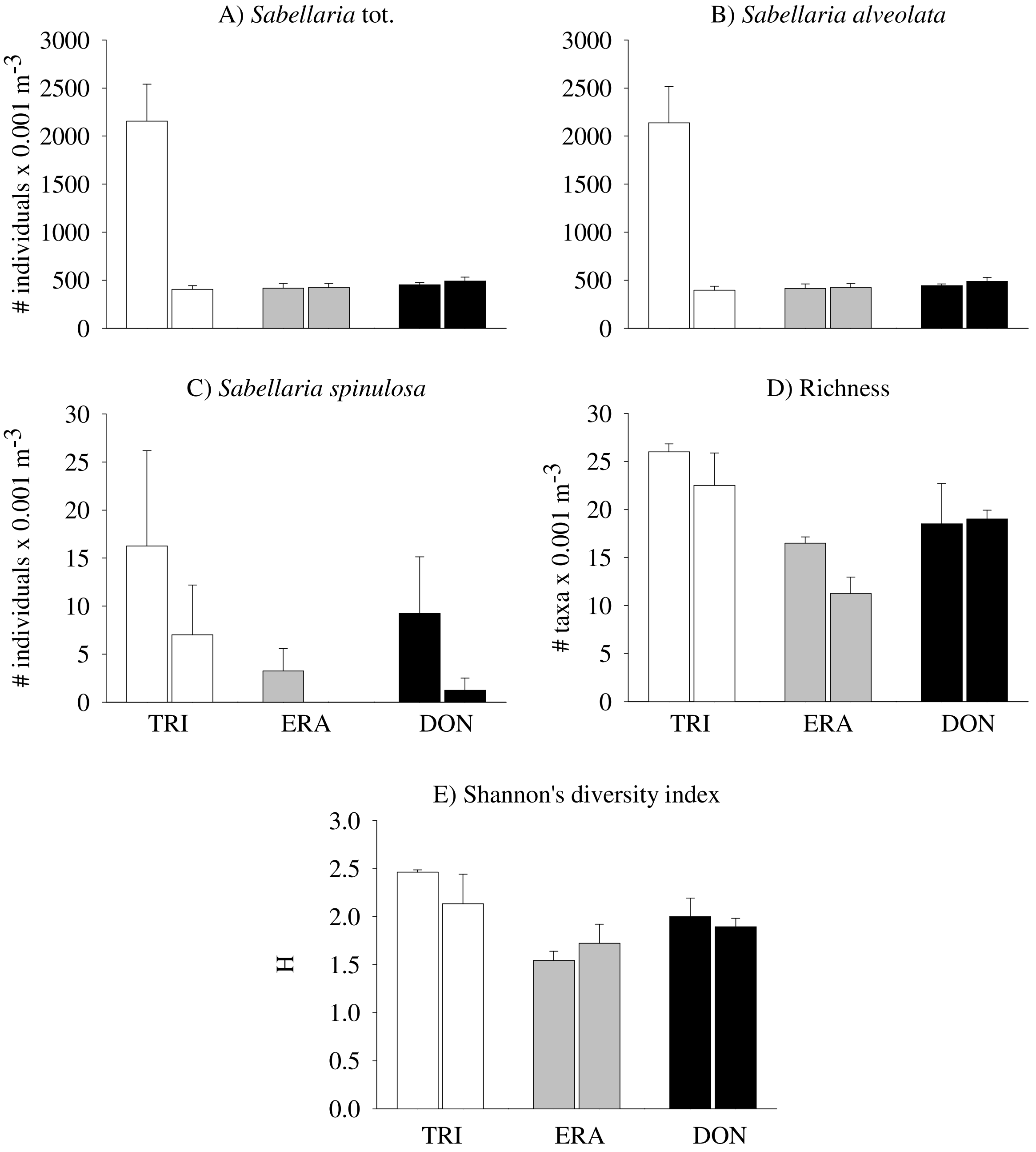
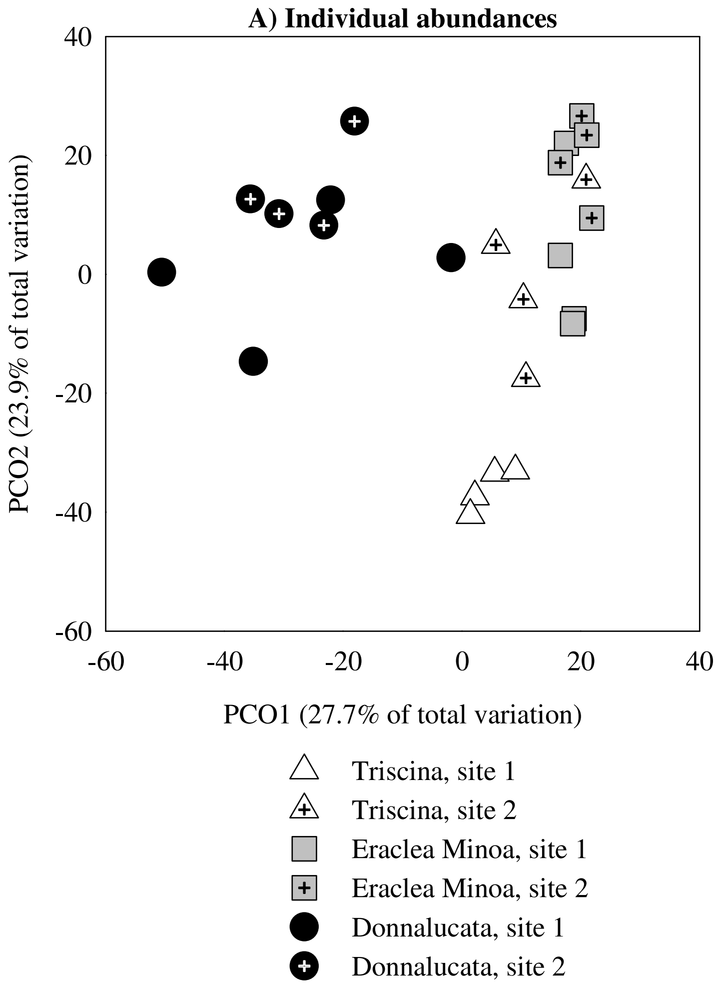


Fig. 1 Bertocci et al.



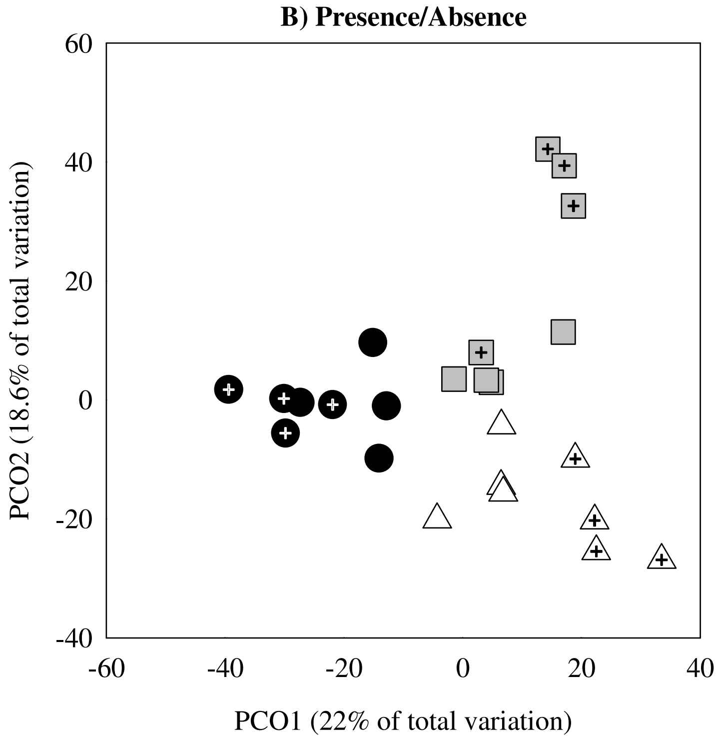


Fig. 2 Bertocci et al.

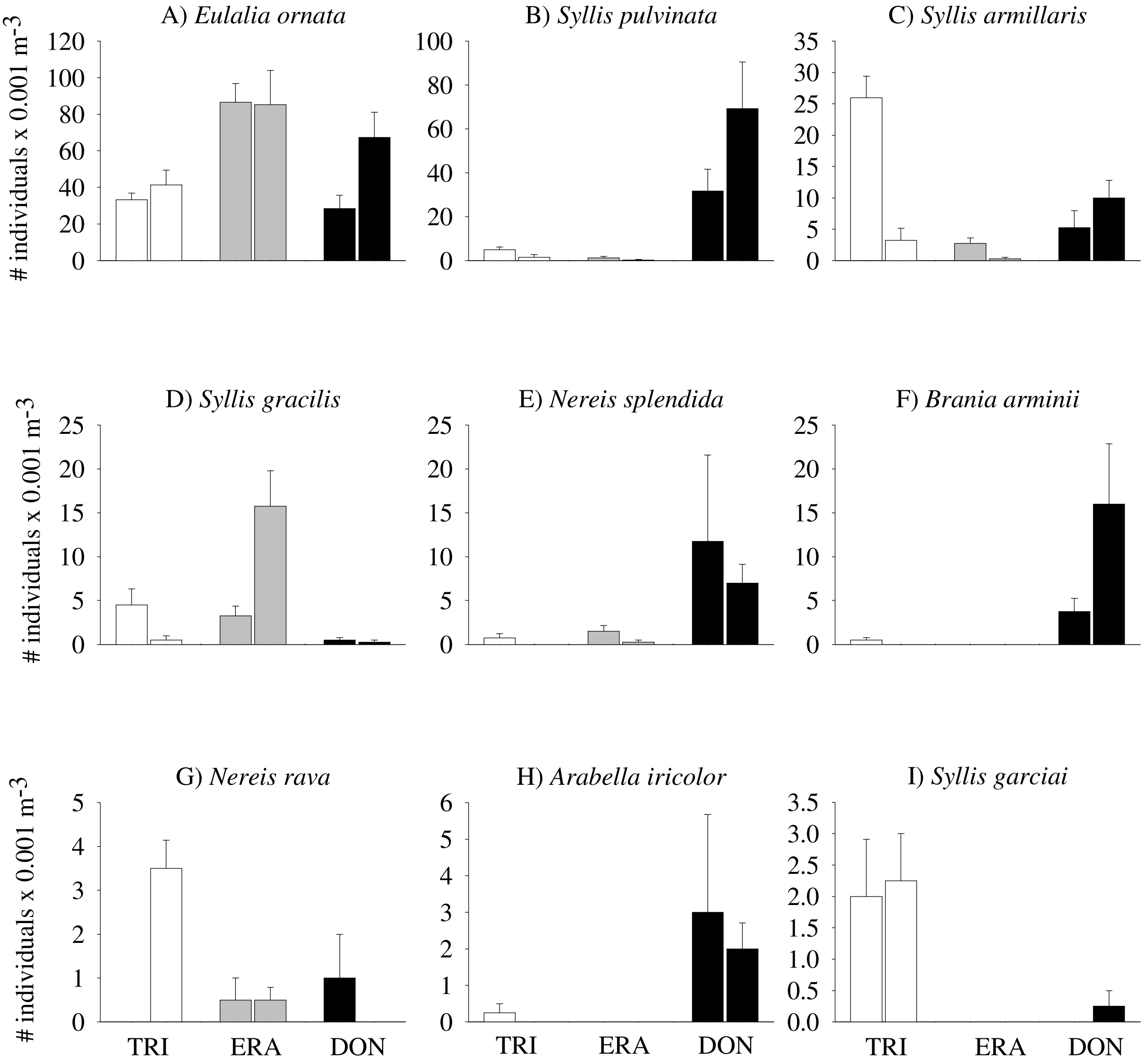


Fig. 3 Bertocci et al.

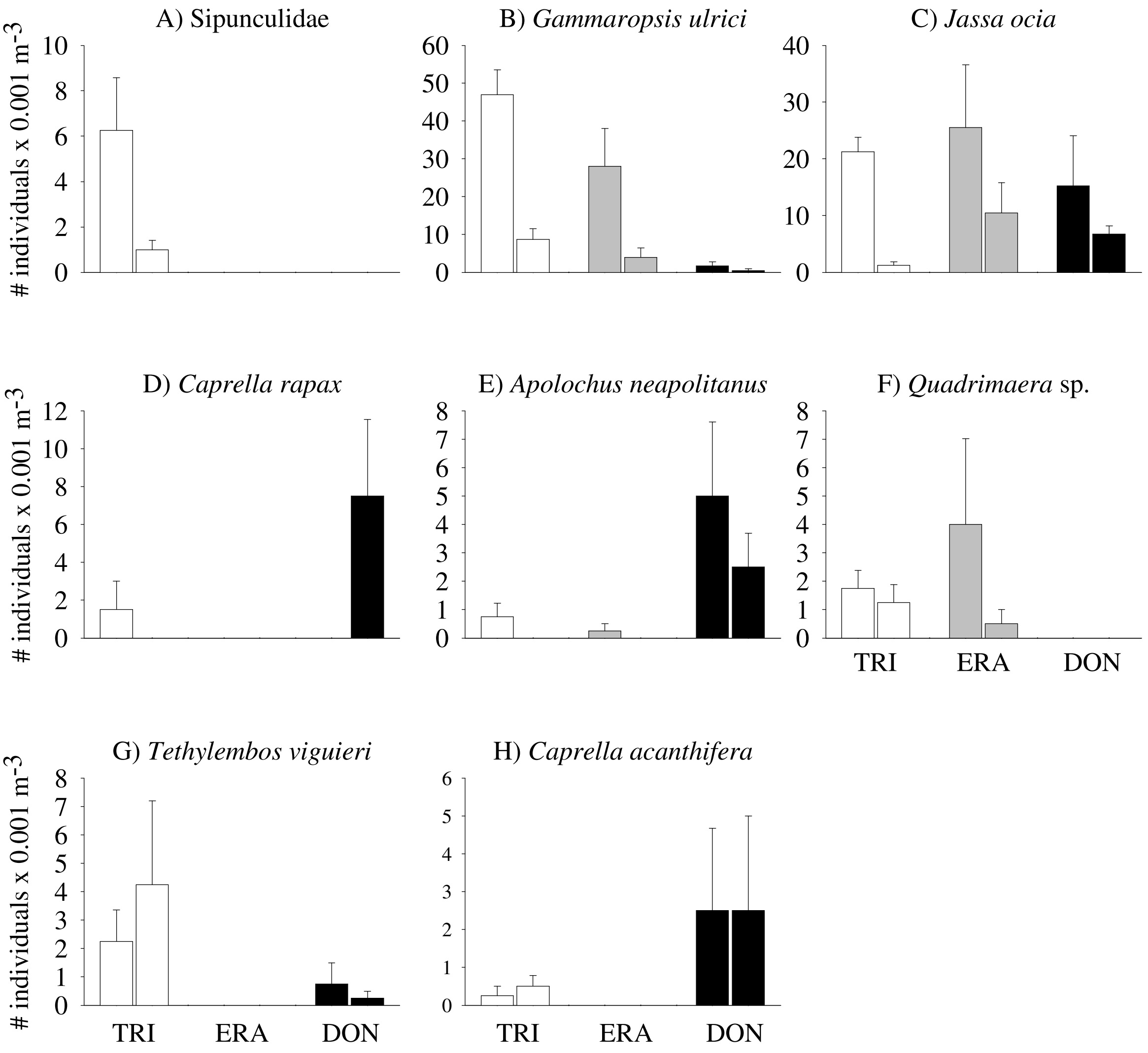


Fig. 4 Bertocci et al.