Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.19732

Consequences of the experimental removal of *Sabella spallanzanii* (Gmelin, 1791) from the fouling assemblage of a Mediterranean harbour

Cataldo PIERRI[1,2,3], Paolo COLANGELO[2], Michela DEL PASQUA[3,4], Caterina LONGO[1,3], Adriana GIANGRANDE[3,4]

[1] Dipartimento di Biologia, Università degli Studi di Bari Aldo Moro, Via Orabona 4, 70125 Bari, Italy
[2] Istituto di Ricerca sugli Ecosistemi Terrestri, Consiglio Nazionale delle Ricerche, Via Salaria km. 29.300, 00015 Monterotondo Scalo, Roma, Italy
[3] Consorzio Nazionale Interuniversitario per le Scienze del Mare (CoNISMa), Piazzale Flaminio 9, 00196 Roma, Italy
[4] Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali, Università del Salento. Via Provinciale Lecce-Monteroni, 73100 Lecce, Italy

Corresponding author: michela.delpasqua@unisalento.it

Handling Editor: Agnese MARCHINI

Received: 17 February 2019; Accepted: 12 May 2019; Published on line: 27 August 2019

Abstract

Filter feeding invertebrates are a relevant component of fouling assemblages with a pivotal role in ecological processes, since they improve water quality, enhance habitat heterogeneity and transfer organic matter from the water column to the benthos. They modulate the availability of resources to other species, with effects on the density and behavior of the surrounding macrofauna. The fanworm *Sabella spallanzanii*, one of the largest and most abundant Mediterranean filter feeders, provides a shelter for predation and a secondary substrate for algae and settlement for sessile invertebrates. We tested its role in driving the structure of fouling assemblages, through a removal experiment.

The experiment was one-year-long, with four sampling times. The effect of the removal on the fouling community was marginal in terms of species richness and evenness, while the biomass showed important differences, with a constant increase over time with higher values in the samples containing *S. spallanzanii*. At the end of observations, the biomass reached the value of 3917 g DW m^{-2} in controls and 2073 g DW m^{-2} in treatments. The empty space left by fanworms was not used by other species with similar biomasses. It is possible that the functioning of fouling communities may, in the event of loss of species, fluctuate in terms of biomass mobilization to different compartments, either towards the pelagic compartment or to the detritus chain. In systems with reduced water turnover, this by-pass can have important consequences in terms of stability and ecological balance.

Keywords: Polychaeta; Sabellidae; assemblage development; Biomass; biodiversity; community dynamics.

Introduction

Under the current scenario of global change, marine ecosystems are heavily affected by human activities, from over-exploitation to habitat loss, from pollution to the introduction of alien species, to global warning (Halpern *et al*., 2008; Hoegh-Guldberg & Bruno, 2010; Burrows *et al*., 2011; Doney *et al.,* 2012; Corriero *et al*., 2016). The consequence is a documented decline in biodiversity (Sax & Gaines, 2003; O'Connor & Crowe, 2005; Hawkins *et al*., 2009). Because of such rapid changes in the composition and richness of most ecosystems, theoretical and empirical research in ecology has focused on the relationship between biodiversity and ecosystem functioning (Loreau *et al*., 2003; Hooper *et al*., 2005; Lefcheck *et al*., 2013; Fung *et al*., 2015; Jaillard *et al*., 2018). Most studies have proved that high biodiversity leads to positive effects on ecological processes, whereas a decline in diversity alters a wide range of ecosystem functionalities (Tilman, 1999; Naeem *et al*., 2009; Cardinale *et al*., 2011, 2012; Tilman *et al*., 2012), although the effect seems to be weaker at ecosystem level than at community level (Balvanera *et al*., 2006). Moreover, when assemblages have a high functional redundancy and several species contribute to the same functions, neutral effects may also occur (Hooper *et al*., 2005).

Biodiversity seems to have a minor effect on the biomass of sessile communities, although high richness values can lead to a consistent increase in variability of community properties and resistance and recovery to disturbance or invasion (Stachowicz *et al*., 2007). In sessile communities, filter-feeders can have a major role in

controlling many ecological processes, since their action improves water quality, contributing to both stability and resilience, enhancing habitat heterogeneity and accelerating the migration of chemical elements (Ostroumov, 2005).

Filter-feeders are able to modulate the availability of resources to other species, with a range of effects on density and behaviour of the surrounding macrofauna. They can regulate community structure through an array of physical mechanisms, such as creation of an additional three-dimensional substrate and local changes of hydrodynamic regimes, as well as biological effects such as the transfer of organic matter from the water column to the benthic environment, the creation of feeding currents, and the chemical attraction influencing larval settlement (Osman, 1977, 1987; Cowden *et al*., 1984; Stoner, 1990; Young, 1990; André & Rosenberg, 1991; Short *et al*., 2013). Therefore, some filter feeders can be considered ecosystem engineers and habitat-forming species (Lawton & Jones, 1995; Rabaut *et al*., 2008), for example sponges (Klitgaard, 1995; Longo *et al*., 2017), tube-building polychaetes (Nalesso *et al*., 1995; Moore *et al*., 1998), molluscs (Hall-Spencer & Moore, 2000; Beck *et al.,* 2011) and bryozoans (Wood *et al*., 2012).

The Mediterranean fanworm *Sabella spallanzanii* (Gmelin, 1791), is one of the most abundant sabellid polychaete species in Mediterranean fouling communities. It is a filter feeding worm that colonizes both natural and artificial substrates, often reaching very high densities. It is characterized by fast growth (Giangrande *et al*., 2005) and can form dense canopies of feeding fans, sometimes completely covering the substratum, and affecting the abundance and composition of benthic assemblages (Eckman, 1983; Cummings *et al*., 2001). The importance of these fanworms in ecological processes was suggested by several studies due to the structuring capability within fouling assemblages.

With their feeding activity, fanworms can create a current which may locally influence water flow, altering sediment stability and concentrations of oxygen or organic matter (Young, 1990; André & Rosenberg, 1991; O'Brien *et al*., 2006). Moreover, they can remove organic matter from the water column producing faeces or pseudofaeces released into the sediment, or during the tube building process where the organic matter, compacted with mucus, is definitively removed from the system. Their tubes also provide a shelter from predation to some species and represent a secondary substrate to the growth of algae and sessile invertebrates (Carey & Watson, 1992; Callaway, 2003). In addition, the filtration activity of *S. spallanzanii* leads to the reduction of POM, DOM and bacteria in the water column (Licciano *et al*., 2005, 2007; Stabili *et al*., 2006; Cavallo *et al*., 2007).

During the last years, the introduction from the Red Sea of the polychaete species *Branchiomma luctuosum* (Grube, 1870) has affected *S. spallanzanii* populations in several southern Mediterranean sites (Mastrototaro *et al*., 2015). This alien sabellid, despite ecological requirements similar to *S. spallanzanii* (Mastrototaro *et al.*, 2015), is smaller and has a different growing strategy, not producing a canopy effect.

Taking into account the above considerations, we investigated, through selective removal, the implications that the loss of *S. spallanzanii* may have on fouling community development in terms of specific richness, diversity and biomass.

It must be stressed that functional biodiversity has been often assessed by using mesocosms (e.g., Naeem *et al*., 1994; Petchey, 2003), and only few studies were conducted within natural communities, from which some species were removed (Rossi *et al*., 2008; Wootton, 2010). In particular, *S. spallanzanii* influence on community development was already investigated by manipulative experiments (Holloway & Keough, 2002 a, b), by only removing the adult specimens in an extra Mediterranean biotope where the species had been previously introduced. Indeed, *S. spallanzanii* is native to the Atlantic-Mediterranean region, but in 1990 it was introduced into Australian waters where it reached extremely high abundances, becoming a pest species with profound impact on coastal economic activities (Clapin, 1996), forming communities so dense that they completely clog the aquaculture cage nets. Holloway & Keough (2002a, b) showed that the removal of the polychaete led to major modifications in the structure of the community, with different influences on the various taxonomic groups. After the removal, the settlement of barnacles and bryozoans was favoured, while that of some sponges was inhibited. However, the same results were obtained by these authors when using artificial structures simulating the morphology of this polychaete; this suggests that the structuring effect on fouling assemblages is probably more related to the physical presence of fanworms than to their biological activity.

Our study is the first attempt in evaluating the effects of the disappearance of sabellid worms on the fouling community dynamics, with a study of over one year, since the stage of early colonization.

Materials and Methods

The study area

The study was conducted at Sant'Eligio tourist port (40.478943° N, 17.230630° E), located on the north side of the city of Taranto (South Italy, Fig. 1), along one of the communication channels between the Mar Piccolo and the Mar Grande of Taranto, which opens into the Gulf of Taranto (Ionian Sea). The seabed depth below the docks varies from 5 to 10 meters, the temperature ranges between 12 and 25 °C (source: http://www.michelemossa.it/stazionemeteo.php) and salinity is around 38 *psu*, with small seasonal variations. This study area was selected according to previous research (Pierri *et al*., 2010) showing the local high recruitment of *Sabella spallanzanii*.

At this site, most of the seabed is covered with sludge and mud (Matarrese *et al*., 2004), while natural hard substrates are extremely rare. Therefore, most of the substrates available to sessile communities are represented

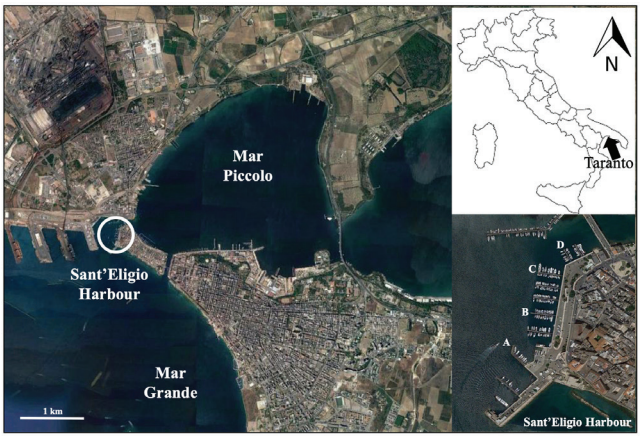

Fig. 1: Map of the study area with a detail of the disposition of the four docks (site A, B, C, D). The Sant'Eligio harbour is located on one of the communication channels between the Mar Piccolo and the Mar Grande of Taranto (Northern Ionian Sea).

by artificial structures that are either floating (docks) or fixed to the bottom (chains, boulders and cement blocks).

Sampling methods

The study was conducted under four randomly selected floating docks out of twelve available, designated as sites A, B, C and D. Twenty-four panels were plunged at approximately 4 m of depth at each site and fixed to horizontal ropes connected to quay chains, arranged in two rows with a distance of approximately 1.5 meters, with a total of 96 panels.

Panels consisted of a PVC net with a 0.5 cm mesh, supported by plastic coated wire to prevent the collapse of the structure because of the weight of fouling species (Fig. 2). We decided to use large net panels (40 x 40 cm) allowing the passage of currents, rather than the classic (15 x 15 cm) PVC panels, in order to intercept a higher number of rare and small organisms.

Panels were submerged in November 2011 in order to allow the recruitment of *Sabella spallanzanii* larvae, which are known to be released in winter (Giangrande *et al*., 2000). Starting from January 2012, panels were checked to verify if the settlement successfully occurred. In March 2012 (T1), some tubes of juvenile polychaetes were recognisable on the nets (i.e. at least 1 cm of length), then removed from half of the panels. The manipulation was performed underwater, by removing thin tubes with tweezers to avoid damaging fanworms and other organisms. Hence, the factor 'treatment' (fixed) had two levels: S- (treatment: samples without *S. spallanzanii)*, and S+ (control: samples with *S. spallanzanii*).

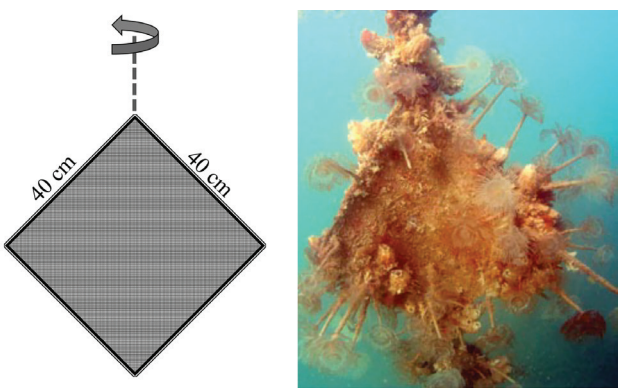

Fig. 2: Plastic mesh panel supported by the plasticized metal frame to prevent collapse. The image on the right shows a panel of the second year with recruited *Sabella spallanzanii* and several solitary ascidians.

Starting in March, sampling was conducted every three months: June (T2); September (T3); December (T4). A total of six panels, three for each treatment (S- and S+), was collected for each site and sampling time, fixed in 5% buffered formalin and brought into the laboratory for further analysis. The investigated side of the panel was randomly chosen to avoid errors due to subjective choices. Before laboratory observations, the panels were submerged in freshwater and then in seawater to remove residual formalin. A reference grid of 100 squares was used for coverage estimation, where each square gave 1% contribution to total coverage. For each panel the number of target species was measured and the variation of such number over time was used as a proxy for mortality. Taxonomic identification of sessile species and relative coverage estimation were performed with no different treatment of colonial or solitary species within each square. The minimum value was rated at 0.25% in relation to the observer's ability to identify coverage values. An arbitrary value of 0.25% was assigned to the presence of small and rare species, when it was not possible to evaluate the contribution to the coverage. After taxonomic identification, organisms were removed, dried at 60°C for 24 hours (until constant weight was reached) and weighted in order to obtain biomass. Biomass was measured considering both surfaces (320 cm^2) to avoid measurement errors due to the removal of organisms from one of the two sides of the panels (160 cm^2).

Data processing

Collected data on both treatment and control samples was used to create a sessile species frequency matrix. It additionally featured biomass (grams of dry weight), richness (number of species and Shannon-Weaver index) and fouling community composition at every sampling time. In order to have comparable results for both control (S-) and treatment (S+) samples, the biomass of all samples never included *S. spallanzanii*.

Initially, the univariate data was tested with asymmetric analysis of variance (ANOVA), conducted in order to test the hypothesis of significant differences in terms of number of recruits among the 4 sites and between the beginning and the end of observations.

The influence of time and treatment on community diversity measured through the variation of specific richness and Shannon-Weaver index (Shannon & Weaver, 1949) was evaluated using a Generalized Linear Mixed Model (GLMM). In this model, sites were considered as a random effect, in order to mitigate the potential spatial

heterogeneity of *S. spallanzanii* recruitment and community composition. Four models were evaluated: 1) a full model including two fixed effects, time and control/treatment as well as their interaction; 2) a model built taking into consideration the additive effect of two factors (no interaction); 3) a model including only time; 4) a model only considering treatment. Using the AIC test, the model that best explains the change in diversity indexes (richness and Shannon-Weaver index) was chosen through the comparison of four models and a null model. Successively, differences between community composition over time and treatment were evaluated using Principal Component Analysis (PCA) on the frequency matrix. The significance of observed differences was tested using a two-way PERMANOVA (9999 replications). Finally, GLMMs were used to evaluate biomass changes in response to time and treatment. To evaluate which factor best explains changes in biomass, the above described model-testing procedure was also repeated using diversity indexes as response variables in which the site was always included as a random effect.

All statistical analyses were performed within the R statistical environment. Generalized linear mixed models were performed using the R package lme4. PERMANOVA was performed using the RVAideMemoire package.

Results

Recruitment of Sabella spallanzanii

The number of specimens was counted just after recruitment period (T1) and in the last sampling period (T4), so that mortality rate could be assessed. Recruitment was highly variable (Fig. 3, Table 1) even at small spatial scales (sites, distance from 30 to 50 meters), ranging from approximately 500 (A, C and D) to more than 3000 ind m^{-2} (site B) (values refer to the real data). In the last sampling event and at all sites, a decrease in the total number of individuals was recorded. Mortality rates varied between 25 and 29% at sites A, C and D, while at site B a mortality up to 65% was recorded, although the density of individuals remained very high at T4 (up to 1000 ind m^{-2}).

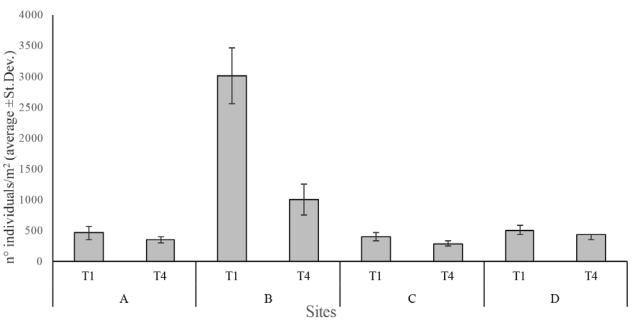

Fig. 3: Individuals (average ± St. Dev.) of *Sabella spallanzanii* recorded at four sites, at the beginning (T1) and the end (T4) of the experiment.

Fouling diversity

A total of 67 taxa (Table S1 - supplementary material) was identified including 18 algae and 49 invertebrates. As expected, a continuous increase in the number of species was observed: at T1, 19 taxa were recorded, followed by a stasis at T2 and T3, and then the number increased reaching 47 taxa at T4. The fouling community was composed of three functional groups, each related to a different feeding guild. Suspension feeders were numerically the most abundant group with 42 taxa (63% *circa* of the total richness). Among them, bryozoans were the most frequent, with 12 species in the fouling community, and had a final total abundance (coverage at T4) of 13.7%. Ascidians were the second most frequent group, with 12 species and a total abundance of approximately 30.7%. Nine species of molluscs were also present in addition to five species of polychaetes. Other taxa, with four species, accounted for no more than 5% of the total abundance.

Primary producers (18 species) accounted for 27% of the community total richness. Among these, red algae with 11 species were the most diverse group. Predators were represented by seven species of hydroids.

According to GLMMs outcomes, the best fitting model for the explanation of diversity changes in fouling assemblage is the one that includes only time as a predictor (Table 2). No changes in General Richness have been observed in the presence/absence of *Sabella*. This was confirmed by the AIC model, which showed the lowest score when the time was considered as the only fixed effect. The same result was obtained by investigating the Shannon-Weaver index.

In both richness and Shannon-Weaver index, estimated values increased from T1 to T2, remained stable at T3 and then increased again at T4. For this reason, only

Table 1. Results of the ANOVA test on the number of specimens of *Sabella spallanzanii* between Site (S) and Time (T). No Transformation has been applied to data.

Source	SS	DF	MS	F	P	F versus
T	366548.1667	1	366548.1667	48.75	0.0000	RES
S	1491868.5000	3	497289.5000	11.61	0.0370	TXS
TXS	128523.1667	3	42841.0556	5.70	0.0075	RES
RES	120294.0000	16	7518.3750			
TOT	2107233.8333	23				

SNK TEST on TxS: Site A: T1> T2; Site B: T1>> T2; Site C: T1= T2; Site D: T1= T2.

Table 2. Five different GLMMs (including null model) with Shannon-Weaver index, Species richness and Biomass of the fouling as dependent variables were evaluated. The best-fitting model identified using AIC is indicated with an asterisk.

Model Shannon	DF	AIC	Model Richness	DF	AIC	Model Biomass	DF	AIC
timextreatment	10	100.97982	timextreatment	9	504.6862	timextreatment *	10	1272.6
time+treatment	7	94.78172	time+treatment	7	500.5525	time+treatment	7	1314.6
treatment	4	154.51062	treatment	4	628.1399	treatment	4	1403.0
time *	6	90.22185	time *	6	498.5549	time	6	1354.0
null model	3	150.6	null model	3	626.2038	null model	3	1429.1

values of time variation of specific richness and Shannon-Weaver index were plotted (Fig. 4).

Temporal dynamics of the fouling assemblage

According to the first two dimensions of the PCA (Fig. 5), explaining the 26.45% of cumulative variance (see supplementary Fig. S1 for the species contribution to cumulative variance), shortly after (T1) the removal of *S. spallanzanii*, the two assemblages were quite similar and they appeared grouped on the left part of the score plot. From the second period of observations and throughout the third period, the two sets of panels showed a slight diversification that seems to suggest treatment-independent behaviour. Finally, the divergence between the two assemblages was larger in the fourth period. This pattern suggests that time was the main factor affecting community composition. However, according to the PERMANOVA test, treatment also had an influence on species composition (treatment: $F=1.590$, $p<0.05$; time: $F=12.358$, $p<0.001$; treatment×time $F=1.622$, $p<0.005$), despite this effect was marginal compared to the observed changes through time and was mainly expressed in the last period (Fig. 5).

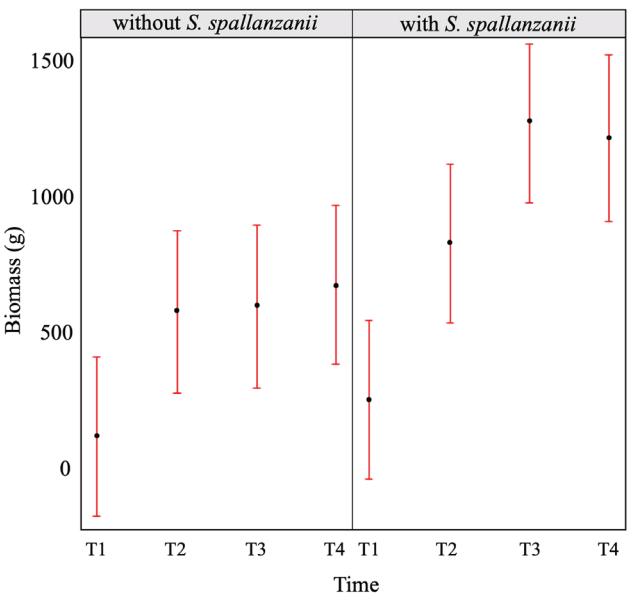

Fig. 4: Diversity pattern in fouling community at four sampling Times (T1, T2, T3, T4), estimated by species richness and Shannon-Weaver index.

The first period of observation (T1) was characterized by the presence of continuous algal felt on S- panels that lasted until T2 (the occurrence frequencies are reported in Table S1 - supplementary material). Starting from T2, communities began to show a modification of coverage in terms of species composition, with some almost monospecific assemblages of the bivalve *Mytilus galloprovincialis* (at station A). However, higher values of mussel coverage (sometimes near 100%) throughout the entire observation period were found only on S+ panels. Even S- panels showed a moderate initial coverage of mussels, but from T3, a detachment of mussel byssus with the opening of several free spots was observed. Ascidians, first appearing at T2, were mostly represented by *Styela plicata* (Lesueur, 1823), subsequently replaced by *Pyura microcosmus* (Savigny, 1816) at T4. Starting from T2, *S. spallanzanii* became abundant, often with values above 50%. The large sabellid *Branchiomma luctuosum* (Grube, 1870) became particularly abundant at the end of the study in both control and treatment samples. The alien calcareous sponge *Paraleucilla magna* Klautau, Monteiro & Borojevic, 2004, was abundant at T4 and was always found on S- panels, together with the bryozoan

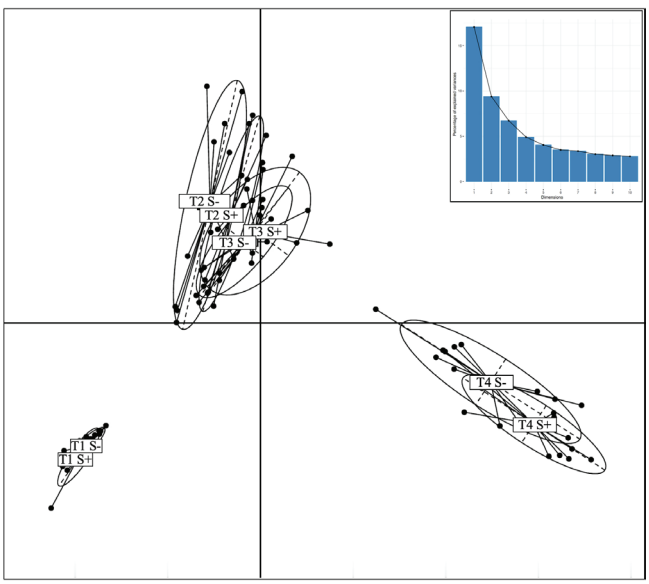

Fig. 5: Result of PCA run on frequency data of the fouling species at four sampling times (T1, T2, T3, T4) for controls (with *Sabella spallanzanii* = S+) and treatments (without *Sabella spallanzanii* = S-). The first two PC axes explain the 17.05% and 9.392% of the total variance, respectively. The explained variance of the first 10 axes are reported in the histogram box.

Schizoporella errata (Waters, 1878).

At T4, the two assemblages were represented by 44 (S+) and 42 (S-) taxa, with approximately the same species composition (80% of overlap). Observed differences were mostly due to the presence of algae (5 taxa) that were numerically more abundant on S+ panels. Regarding the relative frequencies of single species, observed weak variations were not sufficient to describe the treatment-related pattern. Despite present in lower numbers, algae had a higher frequency in treatment samples while *M. galloprovincialis* had higher values in controls during all observation periods. Compared to the control samples in which erect bryozoans were more frequent, solitary ascidians and encrusting bryozoans had slightly higher frequencies in all treatments. All the species of hydroids had higher frequencies in control samples than in treatment ones.

Biomass

As for diversity indexes, biomass increased over time, although a significant influence of treatment has also been observed (Fig. 6, Table 2).

In fact, the best fitting model supported by AIC is the full model in which biomass is explained by the interaction between the presence of *S. spallanzanii* and time of colonization (from T1 to T4). According to this model, biomass increased in controls, from T1 to T3, when it reached a plateau, remaining almost stable up to T4. By contrast, in the treatment sample, the increase in biomass was less continuous and reached a plateau at T2. Generally, at T4, the control reached higher values of biomass compared to treatment. At T1, after one month from fanworm removal, biomass ranged from 333 g DW m^{-2} (SE ± 28) in treatment to 750 g DW m^{-2} (SE ± 80) in controls. Differences between control and treatment remained evident at T2 and T3. At the end of observations, biomass reached the value of 3917 g DW m^{-2} (SE ± 67) in control and 2073 g DW m^{-2} (SE ± 54) in treatment.

In Figure 7, the variation in the relative frequency of occurrences is shown as a function of treatment (S+ and S-) in biomass-forming species. Considering the results of the PCA (Fig. 6), only the last observation period (T4) was chosen and represented in the histogram (Fig. 5); moreover, among all the species present at T4, only those with a large body size were selected because of their capability of producing appreciable biomass (a sponge, two molluscs, three polychaetes, two bryozoans and six ascidians). The selection was necessary for graphic requirements, based on the personal experience of the authors and in relation to biomass, population density and frequency at which the species were found in the fouling in the study area. Among these species, only the mollusc *M. galloprovincialis* showed a significant increase (ANOVA test, F = 11.40878036, $p < 0.05$) in the relative frequency of occurrence (more than double value), while ascidians *Clavelina lepadiformis* (Müller, 1776) (ANOVA test, F = 22.72264994, $p < 0.01$) and *Phallusia mammillata* (Cuvier, 1815) (ANOVA test, F = 12.145719463, $p < 0.05$) showed a decrease when *S. spallanzanii* was present. Two additional ascidians, *S. plicata* and *Ascidiella aspersa* (Müller, 1776), showed an increase in most observations, but it was not statistically significant.

Discussion

This paper investigates the effects of removal of the Mediterranean fanworm *Sabella spallanzanii* during its early colonization stage in a biotope in which the species is naturally abundant and can be considered a structuring taxon dominating the fouling final successions (Pierri *et al*., 2010).

A previous manipulative experiment was conducted along the Australian coastline by removal of the species, stressing an effect more related to the physical presence of fanworm tubes, with the creation of a canopy effect acting on the structure of the community (Holloway & Keough, 2002 a, b). The remarkable impact displayed in

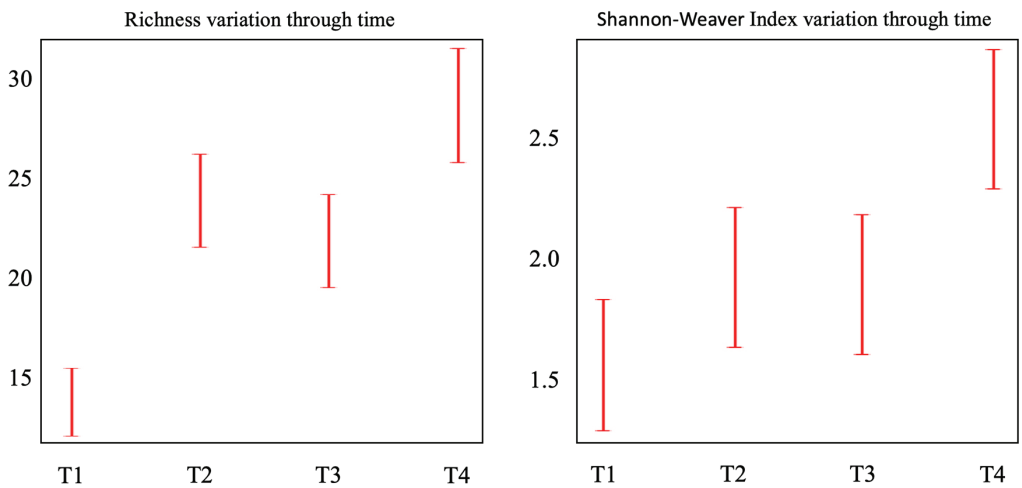

Fig. 6: Relationship between biomass in the experimental conditions (with and without *Sabella*) at four sampling Times (T1, T2, T3, T4). Biomass refers to dry weight (g) *per* panel. Biomass recorded on the both sides of panels (160 cm^2 x 2 = 320 cm^2) was considered to avoid errors due to the handling.

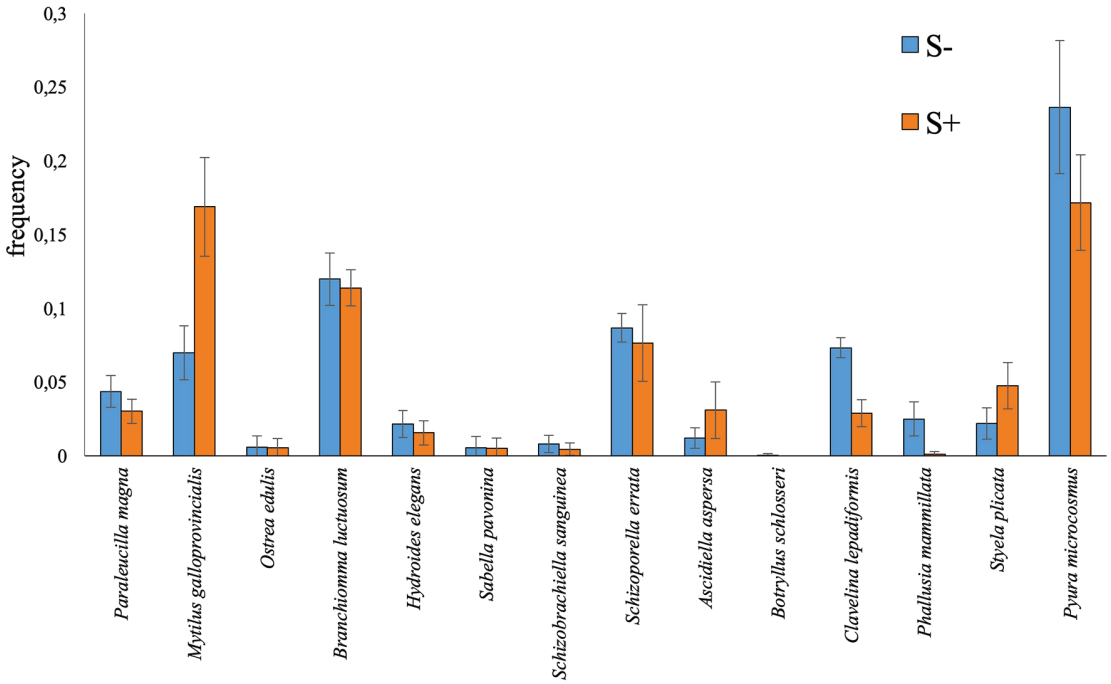

Fig. 7: Frequency of occurrence at the end of observations (T4) of species able to form consistent biomass with (S+) and without *Sabella spallanzanii* (S-). Of all the species present at T4, only those capable to realize appreciable biomass were selected. The selection was based on biomass, population density and occurrence of the species in the fouling of the study area.

its introduction range (Australia, e.g. see Clapin & Evans, 1995; Clapin, 1996), could be explained by the absence of species of similar size and filtering activity in the recipient habitat.

Taking into consideration that global warming is shifting Mediterranean fouling assemblages towards a more tropical connotation, and particularly in the Gulf of Taranto (Cecere *et al*., 2016), we investigated the role of *S. spallanzanii* as structural taxon in its native environment, in order to understand the possible consequences of its disappearance from the fouling community. This scenario has been previously linked to the introduction of the sabellid *Branchiomma luctuosum* (Mastrototaro *et al*., 2015). Since its introduction, in some areas this alien species has caused a reduction of *S. spallanzanii* density. This scenario, however, was not observed in our study area, where the two sabellids seemed to coexist without interference or difficulties in recruitment. Indeed, the recruitment of *S. spallanzanii* appeared massive, in accordance with previous data (Giangrande *et al*., 2000, 2005; Pierri *et al*., 2010), although highly variable within the investigated sites, confirming a still relevant presence of the fanworm within fouling assemblages.

Data from this study revealed that the removal of *S. spallanzanii,* starting from the early stage of colonization, did not have a strong and significant effect on the underlying community biodiversity. The only significant relationship was related to natural temporal dynamics. Despite this, however, it is possible to recognize some feeble influence of the fanworm removal on the occurrence and distribution of different taxa. For instance, algae showed an increase in abundance within treatments, as well as some invertebrates, for example the solitary ascidians *Clavelina lepadiformis* and *Phallusia mammillata* that took advantage of the absence of *S. spallanzanii*. On the contrary, other ascidians and serpulids seemed to be negatively affected by the treatment (S-).

The fanworm presence seems to have a positive influence on *Mytilus galloprovincialis*, one of the most abundant species in the studied biotope, and spatially competing with *S. spallanzanii* (Lezzi *et al*., 2018). It cannot however be excluded that this positive influence may have been mediated by the presence of epibionts on polychaetes tubes.

The role that *S. spallanzanii* plays in structuring the community in the initial phase is related to the persistence of algal felt in treatments, which seems to drive further development of the community, at least within the investigated period. According to Lezzi *et al*. (2018), in fouling assemblages the algal felt is usually quickly replaced during succession, while worms maintain their place becoming dominant in the assemblage, so that other sessile invertebrates, such as ascidians, may be excluded or leastwise negatively influenced, especially in areas with low mussel recruitment rate. In the initial phase of colonization, biological effects produced by the presence of *S. spallanzanii* can be dominant, while physical effects, e.g. the creation of canopy, may become important during the late stages. Biological effects may be mediated by the production of chemical compounds that act as facilitators or inhibitors. It is interesting to underline that *S. spallanzanii* produces mucus with antibacterial activity (Giangrande *et al*., 2013), which can potentially affect the bacterial film and therefore the settlement of different organisms.

In general, the coverage and species richness showed

great variability among treatments as well as among replicates within treatments, not allowing the identification of a significant pattern due to the polychaete removal.

By contrast, as concerns the rest of the fouling assemblage, a strong effect produced by the removal of the fanworms seems to occur on biomass production. At every site, control panels had significantly higher biomasses compared to treatments: it could be hypothesized that the presence of polychaetes promotes an increase in fouling biomass. However, this general pattern (significantly higher biomass in treatments during all the observation periods) presented differences when considering different taxa. In particular, number of mussels presented the largest variation.

The space that had been left available by the fanworms was not colonized by other species with the ability to reach similar biomasses, or with similar features. Other filter feeders able to produce large biomasses observable in the Taranto area are as ascidians, sponges, Mediterranean mussels and other sabellids. However, *S. spallanzanii* is permanently present within the fouling, while ascidians have a seasonal presence with some severe regressions due to high summer temperatures; mussels form dense but fragile communities, because their byssus is not able to sustain considerable weights. Furthermore, the alien sabellid *B. luctuosum* has a different growth strategy (Mastrototaro *et al*., 2015), and cannot substitute the removed species.

Although there is a growing interest in the relationship between ecosystem functioning and biodiversity, the literature on functional biodiversity loss is still rather scarce and often focuses on the effects of introduction of alien species or on the evaluation of inter-specific relations (Poore *et al*., 2012). Other studies, show the effects of canopy-forming algae removal, resulting in an increase in abundance for some species and a decrease for others (Valdiva, 2008). It was also proved that the density of mussel monocultures can influence associated benthic assemblages of adjacent and interstitial sediments, altering species composition and abundance of invertebrate species (Beadam *et al.*, 2004).

The most interesting point that can be drawn from this paper is the effect that the removal of *S. spallanzanii* has on the overall fouling biomass. According to Olam *et al*. (2002), biomass reduction could be caused by a disturbance resulting from the removal of organisms, especially if the disturbance is persistent. The effect of such disturbance on fouling assemblage biomass, was also studied by Wollgast *et al*. (2008) and De Almeida *et al*. (2008). Both showed that the disturbance at the beginning seemed to significantly act on species composition but in the end, it had no effect on species richness and Shannon-Weaver index. Irregular disturbance regimes enhanced the abundance of the ascidian *Ciona intestinalis* (Linnaeus, 1767) biomass production, and total species cover of assemblages. These results, however, derive from the removal of all the species in an assemblage, and not that of a single species.

In this work, even if the disturbance (fanworms removal) could be considered as a random event of low entity, it provides a good indication of what might happen if the disturbance becomes persistent (disappearance of fanworms), causing cascading effects on other taxa that are generally abundant in port environments (for example, molluscs and ascidians). This would result in a further loss of biomass from the filter-feeding benthic compartment, hence influencing the entire surrounding ecosystem (Stabili *et al*., 2006).

Filter-feeding species are effective biofilters and can also naturally mitigate the risk of aquatic diseases for humans and wildlife, which is expected to worsen with climate change, strengthening the need of new strategies to manage the diseases (Burge *et al*., 2014). The currently investigated species was, in fact, already proposed as bioremediator of aquaculture wastes (Stabili *et al*., 2010; Granada *et al*., 2016).

In conclusion, the functionality of Mediterranean fouling communities would certainly be compromised if some of the key species were lost, including *S. spallanzanii* which has neither native nor alien viable substitutes. This study clearly shows that the alteration of benthic biodiversity in eutrophic environments involves a modification of functional parameters such as biomass and the relative frequency of species. The reduction of biomass that was recorded in the benthic filter feeder compartment after the removal of *S. spallanzanii* may not only have repercussions in the fouling community but could also lead to changes in the overall functioning of coastal and lagoon marine ecosystems. However, it must be stressed that biomass cannot be simply lost, but it is probably only transferred, and the total yearly biomass should not significantly vary within multi-annual cycles (Boero *et al*., 1996; Boero, 2008). The standing stock of a given community might be rather constant in time (if no catastrophic perturbations occur), whereas the species might alternate in their contribution to biomass. For both seasonal and perennial species, the mechanism of such turnover is strictly linked to successful recruitment (see member/vagrant hypothesis, Sinclair & Iles, 1989). In this way, the 'functioning' of a community would remain unaltered, but the composition of species having a certain role could change. It is possible that the functioning of a complex system such as fouling could fluctuate in terms of biomass mobilization in different compartments and the biomass lost by fouling could be located somewhere else, in the water column or in the sediments.

Biodiversity, broadly defined, significantly influences the magnitude and variability of ecosystem properties such as community biomass and resource consumption (measured as filtration rate) Nevertheless, the effects of species composition seem to be more important than those of species richness (Valdiva, 2008). The loss or gain of particular species therefore may have a stronger effect on ecosystem stability than species richness *per se*. Therefore, predicting the consequences of biodiversity loss remains complicated, since it requires an accurate knowledge of the system and natural life history and should be drawn from sound experimental evidence, not from generalised models.

Acknowledgements

The authors thank the two anonymous referees and the editor for their valuable advice during the paper review. Thanks also to Tamara Lazic and Connor Thorburn for the linguistic revision and critical reading of the manuscript.

References

André, C., Rosenberg, R., 1991. Adult-larval interaction in the suspension-feeding bivalves *Crastoderma edule* and *Mya arenaria*. *Marine Ecology Progress Series*, 71 (3), 227-234.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T. *et al*., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9 (10), 1146-56.

Beadam, H.A., Kaiser, M.J., Galanidi, M., Shucksmith, R., Willows, R.I., 2004. Changes in species richness with stocking density of marine bivalves. *Journal of Applied Ecology,* 41, 464-475.

Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D. *et al*., 2011. Shellfish reefs at risk globally and recommendations for ecosystem revitalization. *Bioscience,* 61, 107-116.

Boero, F., 2008. Fluctuations and Variations in Coastal Marine Environments. *Marine Ecology*, 15 (1), 3-25.

Boero, F., Belmonte, G., Fanelli, G., Piraino, S., Rubino, F., 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends in Ecology & Evolution*, 11 (4), 177-80.

Burge, C.A., Mark Eakin, C., Friedman, C.S., Froelich, B., Hershberger, P.K. *et al*., 2014. Climate change influences on marine infectious diseases: implications for management and society. *Annual Review Marine Science*, 6, 249-277.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S. *et al*., 2011. The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science*, 334 (6056), 652-655.

Callaway, R., 2003. Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks. *Journal of Experimental Marine Biology and Ecology*, 283 (1-2), 115-132.

Cardinale, B.J., Matulich, K., Hooper, D.U., Byrnes, J.E., Duffy, J.E. *et al*., 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany*, 98 (3), 572-592.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C. *et al*., 2012. Biodiversity loss and its impact on humanity. *Nature*, 486, 59-67.

Carey, J.M., Watson, J.E., 1992. Benthos of the muddy bottom habitat of the Geelong Arm of Port Phillip Bay, Victoria, Australia. *The Victorian Naturalist*, 196-202.

Cavallo, D., Pusceddu, A., Danovaro, R., Giangrande A., 2007. Particulate organic matter uptake rates of two benthic filter-feeders (*Sabella spallanzanii* and *Branchiomma luctuosum*) candidates for the clarification of aquaculture wastewaters. *Marine Pollution Bulletin*, 54 (5), 602-625.

Cecere, E., Petrocelli, A., Belmonte, M., Portacci, G., Rubino, F. 2016. Activities and vectors responsible for the biological pollution in the Taranto Seas (Mediterranean Sea, southern Italy): a review. *Environmental Science and Pollution Research*, 23, 12797-12810.

Clapin, G., 1996. *The filtration rate, oxygen consumption and biomass of the introduced polychaete* Sabella spallanzanii *(Gmelin) Within Cockburn Sound: can it control phytoplankton level and is it an efficient filter feeder?* PhD Thesis. Department of Environmental Management, Edith Cowan University, Joondalup, Western Australia, 90 pp.

Clapin, G., Evans, D., 1995. The status of the introduced marine fanworm *Sabella spallanzanii* in Western Australia: a preliminary investigation. Centre for Research on Introduced Marine Pests, Technical report, No 2, 34 pp.

Corriero, G., Pierri, C., Accoroni, S., Alabiso, G., Bavestrello, G. *et al*., 2016. Ecosystem vulnerability to alien and invasive species: a case study on marine habitats along the Italian coast. *Aquatic Conservation-Marine and Freshwater Ecosystems,* 26 (2), 392-409.

Cowden, C., Young, C.M., Chia, F.S., 1984. Differential predation on marine invertebrate larvae by two benthic predators. *Marine Ecology Progress Series*, 14, 145-149.

Cummings, V.J., Thrush, S.F., Hewitt, J.E., Funnell, G.A., 2001. Variable effect of a large suspension-feeding bivalve on in fauna: experimenting in a complex system. *Marine Ecology Progress Series*, 209, 159-175.

De Almeida Xavier E., Perez De Gama B.A., Porto T.F., Lopes Antimes B., Crespo Pereira R., 2008. Effects of disturbance area on fouling communities from a Tropical environment: Guanabara bay, Rio De Janeiro, Brazil. *Brazilian Journal of Oceanography*, 56 (2), 73-84,

Doney, S., Ruckelshaus, M., Duffy, E.J., Barry, J.P., Chan, F. *et al.,* 2012. Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science*, 4, 11-37.

Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography*, 28 (2), 241-257.

Fung, T., Farnsworth, K.D., Reid, D.G, Rossberg, A.G., 2015. Impact of biodiversity loss on production in complex marine food webs mitigated by prey-release. *Nature Communications*, 6, 6657.

Giangrande, A., Cavallo, A., Licciano, M., Mola, E., Pierri, C. *et al.,* 2005. Utilization of the filter feeder *Sabella spallanzanii* Gmelin (Sabellidae) as bioremediator in aquaculture. *Aquaculture International*, 13 (1-2), 129-136.

Giangrande, A., Licciano, M., Pagliara, P., Gambi, M., 2000. Gametogenesis and larval development in *Sabella spallanzanii* (Polychaeta, Sabellidae) from Mediterranean Sea. *Marine Biology*, 136 (5), 847-861.

Giangrande, A., Licciano, M., Schirosi, R., Musco, L., Stabili, L., 2013. Chemical and structural defensive external strategies in six sabellid worms (Annelida), *Marine Ecology*, (35) 1, 36-45.

Granada, L., Sousa, N., Lopes, S., Lemos, M.F.L., 2016. Is integrated multitrophic aquaculture the solution to the sectors' major challenges? e a review. *Reviews in Aquaculture*, 8 (3), 283-300.

Hall-Spencer, J.M., Moore, P.G., 2000. *Limaria hians* (Mollusca: Limacea): a neglected reef-forming keystone species. *Aquatic Conservation: Marine and Freshwater Ecosys-*

tems, 10, 267-277.

Halpern, B.S., Walbridge, S., Selkoe, K. A., Kappel, C.V., Micheli, F. *et al*., 2008. A Global Map of Human Impact on Marine Ecosystems. *Science*, 319 (5865), 948-952.

Hawkins, S.J., Sugden, H.E., Mieszkowska, N., Moore, P.J., Poloczanska, E. *et al*., 2009. Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series*, 396, 245-259.

Hoegh-Guldberg, O., Bruno, J.F., 2010. The Impact of Climate Change on the World's Marine Ecosystems. *Science,* 328 (5985), 1523-1528.

Holloway, M.G., Keough, M.J., 2002a. An introduced Polychaete affects recruitment and larval abundance of sessile invertebrates. *Ecological Applications*, 12 (6), 1803-1823.

Holloway, M.G., Keough, M.J., 2002b. Effects of an introduced polychaete, *Sabella spallanzanii*, on the development of epifaunal assemblages. *Marine Ecology Progress Series*, 236, 137-154.

Hooper, D.U., Chapin, F.S.I., Ewel, J.J., Hector, A., Inchausti, P. *et al*. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75 (1), 3-35.

Jaillard, B., Deleporte, P., Loreau, M., Violle, C., 2018. A combinatorial analysis using observational data identifies species that govern ecosystem functioning. *PLOS ONE,* 13(9), e0203681.

Klitgaard, A.B., 1995. The fauna associated with outer shelf and upper slope sponges (Porifera: Demospongiae) at the Faroe Islands, northeastern Atlantic. *Sarsia*, 80, 1-22.

Lawton, J.H., Jones, C.G., 1995. Linking species and ecosystems: organisms as ecosystem engineers. p. 141-150. In: *Linking species and ecosystems,* Jones, C.G., Lawton, J.H. (Eds). Chapman & Hall, Inc., New York, USA.

Lefcheck, J.S., Whalen, M.A., Davenport, T.M., Stone, J.P., Duffy, J.E., 2013. Physiological effects of diet mixing on consumer fitness: a meta-analysis. *Ecology,* 94 (3), 565-572.

Lezzi, M., Del Pasqua, M., Pierri, C., Giangrande, A., 2018. Seasonal non-indigenous species succession in a marine macrofouling invertebrate community. *Biological Invasions*, 20 (4), 937-961.

Licciano, M., Stabili, L., Giangrande, A., 2005. Clearance rates of *Sabella spallanzanii* and *Branchiomma luctuosum* (Annelida: Polychaeta) on a pure culture of *Vibrio alginolyticus*. *Water Research*, 39 (18), 4375-4384.

Licciano, M., Terlizzi, A., Giangrande, A., Cavallo, R.A., Stabili, L., 2007. Filter-feeder macroinvertebrates as key players in bacterioplankton biodiversity control: a case of study with *Sabella spallanzanii* (Polychaeta: Sabellidae). *Marine Environmental Research,* 64 (4), 504-513.

Longo, C., Cardone, F., Pierri, C., Mercurio, M., Mucciolo, S. *et al*. 2017. Sponges associated with coralligenous formations along the Apulian coasts. *Marine Biodiversity*.

Loreau, M., Mouquet, N., Gonzalez, A., 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences*, 100 (22), 12765-12770.

Matarrese, A., Mastrototaro F., D'Onghia, G., Maiorano, P., Tursi A., 2004. Mapping of the benthic communities in the Taranto seas using side-scan sonar and an underwater video camera. *Chemistry and Ecology*, 20 (5), 377-386.

Mastrototaro, F., Chimienti, G., Matarrese, A., Giangrande, A., 2015. Growth and population dynamics of the non-indigenous species *Branchiomma luctuosum* Grube (Annelida, Sabellidae) in the Ionian Sea (Mediterranean Sea). *Marine Ecology*, 36 (3), 517-529.

Moore, C.G., Saunders, G.R., Harries, D.B., 1998. The status and ecology of *Serpula vermicularis* L. (Polychaeta: Serpulidae) in Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 8, 645-656.

Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C.H., 2009. Introduction: the ecological and social implications of changing biodiversity. An overview of a decade of biodiversity and ecosystem functioning research. p. 3-13. In: *Biodiversity, ecosystem functioning, & human wellbeing*. Naeem, S., Bunker, D.E., Hector, A., Loreau, M. Perrings, C.H. (Eds.). Oxford University Press.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., Woodfin, R.M., 1994. Declining biodiversity can alter the performance of ecosystems. *Nature*, 368 (6473), 734-737.

Nalesso, R.C., Duarte, L.F.L., Pierozzi, I., Enumo, E.F., 1995. Tube epifauna of the polychaete *Phyllochaetopterus socialis* Claparéde. *Estuarine, Coastal and Shelf Science*, 41, 91-100.

O'Brien, A.L., Ross, D.J., Keough, M.J., 2006. Effects of *Sabella spallanzanii* physical structure on soft sediment macrofaunal assemblages. *Marine and Freshwater Research,* 57 (4), 363-371.

O'Connor, N.E., Crowe, T.P., 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology*, 86 (7), 1783-96.

Olam, S.G.B, Ernandes, T.F.F, Uxham, M.H., 2002. Diversity, Biomass, And Ecosystem Processes in The Marine Benthos. *Ecological Monographs*, 72 (4), 599-615.

Osman, R.W., 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs*, 47, 37-63.

Osman, R.W., 1987. Interactions between the vermetid *Serpulorbis squamigeras* (Carpenter) and several species of encrusting bryozoans. *Journal of Experimental Marine Biology and Ecology,* 111, 267-284.

Ostroumov, S.A., 2005. Some aspects of water filtering activity of filter-feeders. *Hydrobiologia*, 542 (1), 275.

Petchey, O.L., 2003. Integrating Methods That Investigate How Complementarily Influences Ecosystem Functioning. *Oikos*, 101 (2), 323-330.

Pierri, C., Longo, C., Giangrande, A., 2010. Variability of fouling communities in the Mar Piccolo of Taranto (Northern Ionian Sea, Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom*, 90 (1), 159-167.

Poore, A.G.B., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V. *et al.,* 2012. Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letter*s 15, 912-922.

Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M., Degraer, S., 2008. A bioengineered soft-bottom environment: the impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuarine Coastal and Shelf Science*, 75 (6), 525-536.

Rossi, F., Gribsholt, B., Middelburg, J.J., Heip, C., 2008. Context-dependent effects of suspension feeding on intertidal ecosystem functioning. *Marine Ecology Progress Series*, 354, 47-57.

Sax, D.F., Gaines, S.D., 2003. Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution*, 18 (11), 561-566.

Shannon, C.E., Weaver, W., 1949. *The mathematical theory of communication.* The University of Illinois Press*,* Urbana*,* 117 pp.

Short, J., Metaxas, A., Daigle, R.M., 2013. Predation of larval benthic invertebrates in St George's Bay, Nova Scotia. *Journal of the Marine Biological Association of the United Kingdom*, 93(3), 591-599.

Sinclair, M., Iles, T.D., 1989. Population regulation and speciation in the oceans. *Journal of Marine Science*, 45 (2), 165-175.

Stabili, L., Licciano, M., Giangrande, A., Fanelli, G., Cavallo, R.A., 2006. *Sabella spallanzanii* filter-feeding on bacterial community: Ecological implications and applications. *Marine Environmental Research,* 61 (1), 74-92.

Stabili, L., Schirosi, R., Licciano, M., Mola, E., Giangrande, A., 2010. Bioremediation of bacteria in aquaculture waste using the polychaete *Sabella spallanzanii*. *New Biotechnology*, 27 (6), 774-781.

Stachowicz, J.J., Bruno, J.F., Duffy, J.E., 2007. Understanding the Effects of Marine Biodiversity on Communities and Ecosystems. *Annual Review of Ecology Evolution and Systematics*, 38, 739-766.

Stoner, D.S., 1990. Recruitment of a tropical ascidian: relative importance of pre-settlement versus post-settlement processes. *Ecology*, 71 (5), 1682-1690.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80 (5), 1455-74.

Tilman, D., Reich, P.B., Isbell, F., 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences of the United States of America*, 109 (26), 10394-10397.

Valdiva N., 2008, Effects of biodiversity on ecosystem stability: distinguishing between number and composition of species. Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften Vorgelegt dem Fachbereich Biologie/ Chemie der Universität Bremen von pp. 147.

Wollgast, S., Lenz, M., Wahl, M., Molis, M., 2008. Effects of regular and irregular temporal patterns of disturbance on biomass accrual and species composition of a subtidal hard-bottom assemblage. *Helgoland Marine Research,* 62 (4), 309-319.

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.

Wootton, J.T., 2010. Experimental species removal alters ecological dynamics in a natural ecosystem. *Ecology*, 91 (1), 42-48.

Young, C.M., 1990. Larval predation by epifaunal on temperate reefs: scale, power and the scarcity of measurable effects. *Australian Journal of Ecology*, 15 (4), 413-426.