Hydrobiologia (2021) 848:4815–4835
https://doi.org/10.1007/s10750-021-04675-x

PRIMARY RESEARCH PAPER

What ecological and functional changes follow the positioning of an artificial barrier? Answers from a 4-year investigation on soft bottom benthic communities

Michela D'Alessandro · Federica Nasi · Larissa Ferrante · Salvatore Giacobbe

Received: 4 March 2021 / Revised: 31 July 2021 / Accepted: 2 August 2021 / Published online: 26 August 2021

Abstract Increasing employment of artificial barriers to combat coastal erosion is causing alterations of coastal ecosystems. Understanding their ecological functioning is key to planning management activities and minimising their negative impacts on the ecosystem. In this paper, changes in biodiversity and in functional traits of macrofaunal shallow communities were investigated throughout 4 years of study in the central Mediterranean. Biodiversity indices (S, d, H′) showed the highest mean values during *in-operam* phases (5.7, 1.99 and 2.07, respectively) whilst functional diversity (FDis) and functional redundancy (FDiv/H′) showed the highest mean values in *ante-operam* (4.34 and 2.44, respectively). The PERMANOVA showed differences both in species composition and functional traits between sampling periods. β-diversity was driven by the replacement of species over years. The non-indigenous polychaete *Lumbrinerides neogesae,* recorded for the first time during *in-operam*, supplied the highest differences between years (14.5%, SIMPER). During *in* and *post-operam* phases an increase of *sub-surface deposit feeder*, *tolerant,* and *pioneer* categories was recorded. When the classic taxonomic approach is combined with novel functional biodiversity attributes, a wide range of biota responses to a disturbance can be better described and the efficient mitigation solutions to minimize negative impacts of human activities proposed.

Keywords Functional traits · β-diversity · Coastal defence · Non-indigenous species · Macrofaunal invertebrates · Thyrrenian sea

Handling editor: Jonne Kotta

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-021-04675-x.

M. D'Alessandro · F. Nasi (✉) · L. Ferrante
National Institute of Oceanography and Applied Geophysics – OGS, via A. Piccard 54, 34151 Trieste, Italy
e-mail: fnasi@inogs.it

S. Giacobbe
Department of Biological and Environmental Science, University of Messina, Viale Stagno d'Alcontres, 31, S. Agata, 98166 Messina, ME, Italy

Introduction

Coastal areas play a crucial role in the economic, social, and political development of most countries, providing valuable goods and services for human health (McLachlan & Defeo, 2017; Austenet al., 2019). Indeed, these environments, which include some of the most biodiverse ecosystems in the world, provide direct economic benefits to humans by supporting industries such as fishing, tourism, and recreation (Remoundou et al., 2009). However, over the past decades, the increase of coastal activities and population is threatening these environments and their benefits, accelerating sea-level rise and land subsidence (Klunder et al., 2020; Navarro et al., 2020). To counter the increasing rate of coastal erosion, the use of artificial structures is common in seascapes throughout the globe (Firth et al., 2016). These constructions have physical, chemical, and biological effects on the coastal ecosystem. Regarding abiotic parameters, artificial structures can alter the natural wave activity, affecting longshore transport and sediment deposition as well as the organic matter availability in sediments (Ambrose & Anderson, 1990; Klunder et al., 2020). In addition, these structures modify light intensity and pollutant amounts by leaching chemicals (Barros et al., 2001; Dugan et al., 2011; Dafforn et al., 2015; Heery et al., 2017; O'Shaughnessy et al. 2020). Regarding biological changes, these systems, considered as stepping stones and/or corridors, favour recruitment, dispersion and connectivity amongst species (Bishop et al., 2017). Different studies were focused on the macrofauna community inhabiting the artificial hard substrata, investigating the rate of colonization (Joschko et al., 2008) and substrata shaping by autogenic ecosystem engineers (Mendez et al., 2015; Deidun et al., 2016). Moreover, the installation of barriers could favour the expansion of opportunistic and non-indigenous species (NIS) (Bulleri & Airoldi, 2005; Perkol-Finkel et al., 2012; Airoldi et al., 2015; Spagnolo et al., 2019).

The installation of artificial barriers is also able to modify a wide range of ecosystem functions (Reeds et al., 2018). In this regard, Biological Trait Analysis (BTA) is a useful analytical approach that looks beyond the mere identity of communities' taxa and focuses more on their functional roles in shaping the ecosystem properties. BTA combines structural data of a macrofaunal community (i.e., species abundance or biomass) with the information on functional features of species (Bremner et al., 2006; Beauchard et al., 2017). Furthermore, functional diversity connects species and related ecosystem processes to environmental fluctuation and community dynamics (Gerisch et al., 2012; Scheiner et al., 2017). Changes in functional diversity are related to the biological traits that occur in species communities, and it is known that environmental factors, including anthropogenic pressure, can influence the frequencies and composition of the traits (Normandin et al., 2017; Piano et al., 2017). The analysis of the relationships between traits and environment, therefore, may help to identify species from pools of regional species able to cope with environmental conditions in the habitats of interest (Moretti et al., 2017). Recently, more studies applied the BTA approach to better understand the influence of natural and human impacts on macrofaunal communities (e.g., Bolam et al., 2016; Nasi et al., 2018) and ecosystems to evaluate conservation and management efforts (Beauchard et al., 2017). After the installation of barriers, a reduction of the percentage of filter-feeding organisms, a decrease of genetic diversity, and changes to the early stages of succession, comprising opportunistic, weedy, and invasive species, have been reported (Chapman, 2003; Fauvelot et al., 2009; Airoldi and Bulleri, 2011). However, so far, the BTA analyses have been poorly utilised to study macrofaunal communities near coastal defences (Munari, 2013), and they have not yet been properly investigated during the artificial defence construction.

In this study, we focused on macrofaunal invertebrates along with spatial scales over a 4-year period. Particular attention was made to the three phases of reef placement: *ante-*, *in-* and *post-operam*. In addition, the BTA was conducted together with the analyses of α- and β- diversity. The α- diversity refers to biodiversity and its components (richness, diversity and evenness), at each sampling site and time, whereas the β-diversity (or turnover) looks at two distinct processes: the replacement and the loss or gain of species. Since previous evidence indicates that artificial structures can facilitate the recruitment of non-native species, in this study we considered the β-diversity to better describe the ecological process of species replacement along the spatial and temporal scale (Whittaker, 1960; Airoldi et al., 2015). In this study, we aimed to assess the macrofaunal community diversity and functional identity influenced by artificial barriers placement over multiple years. In particular, the following hypotheses have been tested: (i) species composition could vary during the three phases of barrier placement, favouring the success of opportunistic and invasive species in marine systems at the expense of pre-existent species; (ii) functional traits occurrences could show a switch, especially in categories belonging to colonization and adult feeding habit; and (iii) the trend of α- and β- diversity indices could reflect these changes showing more variations during *in-operam* phase.

Material and methods

Study area

The study area, within the municipality of Villafranca Tirrena, is located halfway up the Gulf of Milazzo (Sicily, Tyrrhenian Sea, Western Mediterranean Sea), which extends about 25 km eastward of the homonymous cape (Fig. 1). This basin houses an international harbour, oil refineries, thermal power plants, and shipbuilding industry, with intensive national and international maritime traffic (D'Alessandro et al., 2016). The study area is subject to irregular inputs by a packed drainage system of short length seasonal rivers, locally named 'Fiumara'. River loads are driven by a prevalent eastward coastal drift, although a near coast anticyclonic gyre is responsible for a westernmost accumulation area close to Cape Milazzo (Sitra et al., 2009). Such rivers, characterized by a very low regime and dramatically reduced flow during most of the year, extend their beds in underwater canyons, whose heads notch a narrow and steep continental shelf (Sabato & Tropeano, 2004). The investigated seafloors, located between the outlets of the 'Gallo' river (38°14′ 58.91″ N; 15° 26′ 37.80″ E, WGS84) and the 'Santa Caterina' river (38°14′34.52″ N; 15°25′39.89″ E, WGS84), connect two channelized areas, whose morphology is due to sediment gravity flows during river floods and, just 500 m from the coastline, to erosion by delta-derived sediment gravity flows (Gamberi et al., 2014). The seafloors are characterized by a sandbank extending from the coastline to 20 m depth on average, followed by a rapid transition to mixed and mud sediments. The most frequent winds are from the SE and NW; the latter can be very intense in winter and spring (Pepe et al., 2010). Superficial hydrodynamics are characterized by a general cyclonic circulation flowing eastward and by an anticyclonic circulation, locally influenced by morphology and winds, characterizing

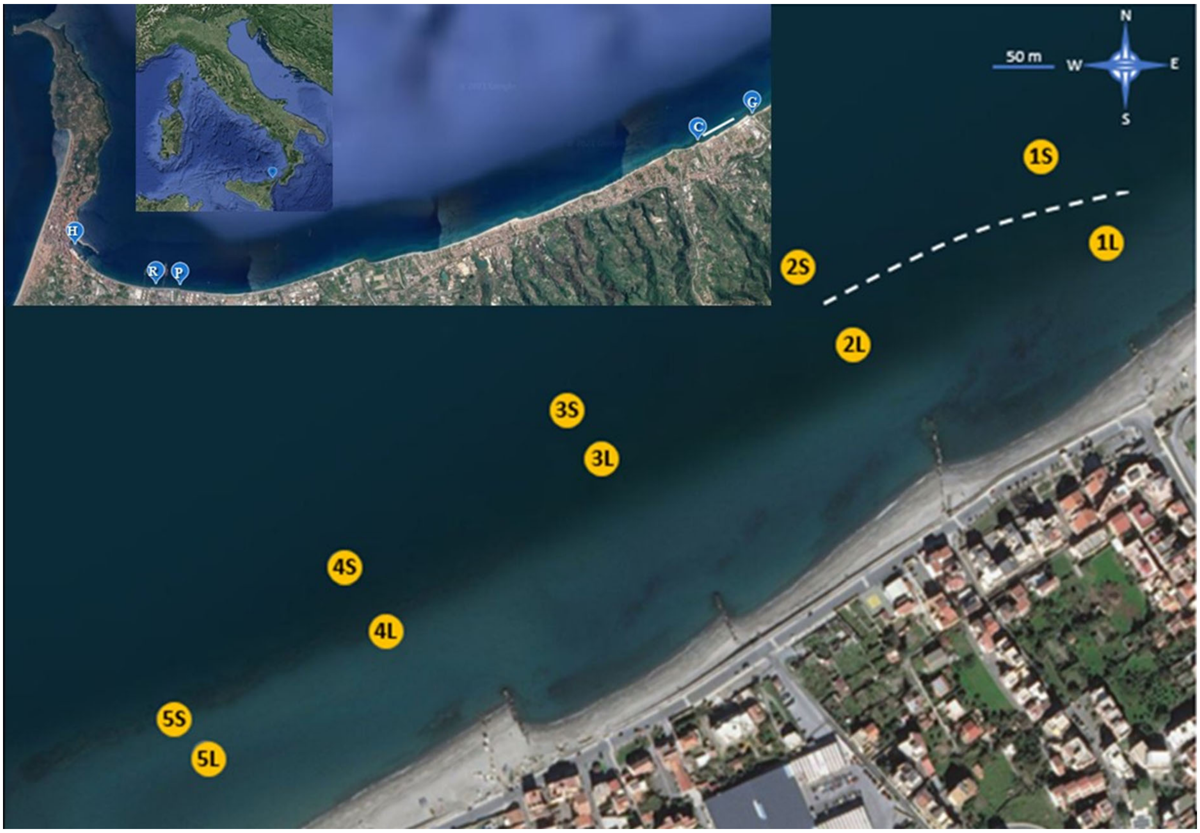

Fig. 1 Study area with the location of the underwater protection barrier (dotted white line) and sampling sites (L: landward; S: seaward). Legend: C, Santa Caterina River; G, Gallo River; H, harbour; P, thermal power plant; R, refinery

the inner sector of the bay (Sitra et al., 2009; Pepe et al., 2010).

Sampling design

Four surveys were conducted to investigate the whole action of barrier placement, from *ante-* (2003), to *in-* (2004–2005), and *post-operam* (2006) phases. Samplings were carried out each year during the month of September at 10 stations along five transects, two of which circumscribed the breakwater outline landward (1L and 2L) and seaward (1S and 2S). The other transects, equally spaced, were located westward up to the Santa Caterina outlet, the only side of the study area with the same granulometric and ecological features (Fig. 1). The whole sampling area, corresponding to the top of a sandbar, showed a 3 ± 0.5 m depth.

Biological and environmental samplings

Macrobenthic fauna was sampled by SCUBA divers, removing a thickness of 20 cm from a 0.25 m^2 sampling surface (Cosentino & Giacobbe, 2008) adequate to supply the 50 dm^3 "minimum volume" of Peres and Picard (1964). Faunistic samples were washed on board, under a gentle seawater flow through a 1 mm mesh sieve, and residues were fixed in 70% alcohol. Macrofaunal organisms were identified at the lowest possible taxonomic level (up to the species level in most cases) using a stereomicroscope, and their absolute counts were investigated.

Grain size and carbonate analysis were conducted on undisturbed sediments, collected using 10 cm diameter corers. The grain size analysis was performed according to Buchanan and Kain (1971), by means of ASTM series sieves spaced 1/2 Φ ($\Phi = -\log2 Ø$, mm), except for the fraction below 63 µm (silt and clay) that was analysed by the column dispersion method. Sediment types were classified according to the ternary Wentworth scale (Wentworth, 1922). Carbonate content was evaluated as $CaCO_3$ percentage, by HCl 1 N treatment and subsequent titration with NaOH 1 N (Barnes, 1959). Organic carbon (Corg) was estimated by employing the chromic acid oxidation technique (Buchanan & Kain, 1971). The grain size fractions and parameters (mean grain size, Mz; mode, Mo; sorting, σ; skewness, Sk; kurtosis, Kg) and carbonate content in sediments ($CaCO_3$) were evaluated to indicate changes in sea bottom energy conditions (Kulkarni et al., 2015). Moreover, the total organic carbon was included as a proxy of organic matter quantity for the macrofaunal community investigated (Table 1).

Biological traits

A total of 10 traits with 34 categories, commonly used in Biological Traits Analysis (BTA) for coastal environments (Tornroos & Bonsdorff, 2012), were considered (Table 1). Moreover, since the study aims to assess the functional changes following the placement of an artificial barrier, we analysed adult, reproductive and larval traits (Table 1). All taxa were coded based on their affinity for the chosen traits using the 'fuzzy coding' procedure (Chevenet et al., 1994). This coding allows for species adherence with multiple categories within each trait (0 = no affinity; 1 = low importance; 2 = moderately high importance; 3 = dominant). Through 'fuzzy coding', taxa can exhibit trait categories to different degrees considering the interspecific variations in trait expressions (Chevenet et al., 1994; Bremner et al., 2006). Traits for each taxon were extracted from literature sources listed in Table S1. The taxonomic resolution was kept at species level whenever possible but adjusted to genus or family when the information on traits was available only at a higher taxonomic level.

Diversities and functional features

The taxonomic α-diversity and its components were assessed on the benthic community throughout space and time (*ante-*, *in-* and *post-operam* phases), calculating three specific indices: (i) Margalef richness-d, (ii) Pielou equitability-J′, and (iii) Shannon–Weaver biodiversity-H′ (Clarke et al., 2014). The temporal variations of macrofaunal diversity were calculated by measuring β-diversity applying the Jaccard dissimilarity index (Villéger et al., 2008). In particular, we investigated whether β-diversity associated with artificial barrier installation was mostly due to turnover (i.e., differences in species amongst years were due to a replacement) or due to nestedness-resultant processes (i.e., species of 1 year represented a subset of those found in the subsequent year). Overall, β-diversity equals 0 when communities are identical and

Table 1 Biological traits, their categories and code

Functional traits	Categories	Code
Reproductive frequency	Semelparous	Sem
	Iteroparous	Iter
	Semi-continuous	Scon
Adult environmental position	Endofauna	Endo
	Epifauna	Epi
	Interface	Inter
	Epibiont	Epib
Adult movement method	Sessile	Sess
	Swimmer	Swim
	Crawler	Craw
	Tube-builder	Tub
	Burrower	Burw
Adult feeding habit	Suspension feeder	Susp
	Surface deposit feeder	Sdep
	Sub-surface deposit feeder	Ssdep
	Herbivore	Hrb
	Carnivore	Crn
Colonization	Pioneer	Pr
	Secondary	Sec
Response to anthropogenic pressure	Sensitive	Sen
	Tolerant	Toll
Larval environmental development	Benthic	Lben
	Pelagic	Lpel
Mechanism development	Direct	Dir
	Lecitotrophic	Flec
	Planktotrophic	Fplan
Types of reproduction	Asex	Asx
	Epitoky	Epit
	Sex:Gonocoric	Sgnc
	Sex: Hermaphrodite	Shrm
Life span	$\leq$ 1 year	Al1
	1–3 years	Al3
	3–6 years	Al6
	6–10 years	Al10

equals 1 when communities are maximally dissimilar (Teixidó et al., 2018 and reference therein).

Regarding functional diversity, the Functional Dispersion (FDis) was calculated based on the fuzzy coding traits and species abundance matrices. FDis describes the abundance-weighted mean distance of individual species to their group centroid (all species community) in multivariate functional space constructed by a principal coordinate analysis (PCoA) based on the Euclidian dissimilarity matrix of species traits (Villéger et al., 2008; Scheiner et al, 2017). Larger FDis values imply a more functionally spread community in the multivariate trait space, and hence a higher functional diversity (Laliberté & Legendre, 2010). In addition, we calculated the functional redundancy (expressed as FDis to Shannon–Wiener ratio-FDiv/H$'$). This index indicates a phenomenon in which multiple species share similar roles in ecosystem functionality (Díaz & Cabido, 2001). Hereby, a higher ratio value is indicative of lower functional redundancy. Lastly, the functional identity was considered to analyse changes in traits composition and occurrences in space and temporal scales. The functional identity as community level weighted means (CWM) of trait category expression was calculated. CWM is a widely used index that may reflect the trait strategies given by the species pool and environmental conditions of a site (Muscarella & Uriarte, 2016). CWM values represent the occurrence of a trait by species in each community, weighted by the abundance of species expressing that specific trait.

Data analysis

Sediment features, species composition, diversity indices, and traits occurrences (CWM values) were compared amongst sampling area and periods. For each test, the following factors were considered, separately: (i) 'sampling years', (ii) 'transects', and (iii) 'stations positions' (i.e., land- and southward). Before all the analyses, data were explored and checked for normality and collinearity (Zuur et al., 2010). Mann–Whitney U and Kruskal–Wallis H (with post hoc comparison) tests were applied as no parametric univariate analyses and one-way PERMANOVA as a multivariate analysis. In the latter test, all the above factors were included as fixed. Furthermore, to assess differences amongst stations influenced by the artificial barrier to those that were not directly affected during the whole study period (from *ante-* to *post-operam* phases) a two-way PERMANOVA main test was carried out. The factor 'artificial barrier' was considered to define the stations directly influenced by barrier placement compared to the others. The latter factor was nested as a fixed factor in the 'sampling years' category. When significant differences were obtained in one- and two-way analyses, the PERMANOVA pairwise tests were performed. Unrestricted permutation of raw data and 9999 permutations were considered.

Further, to point out which taxa majorly contributed to temporal variation of macrofaunal assemblage, SIMPER (SIMilarityPERcentange) one-way analysis was used and factors' 'sampling years' were included. A cut-off at 70% was applied. Similarly, Principal Coordinates Analysis (PCoA) was performed on traits occurrences to highlight differences in functional modalities amongst sampling stations and periods.

In addition, grain size distribution and organic carbon content (as variables that could affect directly macrofaunal distribution), were used to perform the Distance-Linear Modelling (DistLM) to assess which variables explained differences ($P < 0.05$) in species and traits composition (i.e., species abundance and CWM matrices, respectively). Before the analysis, the abiotic parameters were normalized and the option 'All specified' and R^2 were used as the selection procedure and criterion, respectively. For the multivariate analyses, the two matrices (species composition and CWM values) were square root, and the Bray-Curtis similarity was applied.

The taxonomic β-diversity and FDis were computed using the R functions from the 'FD' (Laliberté et al., 2014) and 'betapart' (Baselga et al., 2017) R packages (R v 3.6.3, R Development Core Team, 2020). Univariate analyses were carried out using STATISTICA 7. Lastly, diversity indices and multivariate analyses were performed using PRIMER 7 (PRIMER-E Ltd. Plymouth, UK) (Clarke et al., 2014).

Results

Biological and environmental results

The entire sampling area was characterised by medium-fine sands throughout the sampling (Mz from 1.5 to 2.0 Φ). The grain size distribution varied slightly from fine sand (1C in 2004) to coarse grains (5L in 2005; 5C and 5L in 2006). In particular, fine-sandy sediments were noticed at stations near the barrier after its placement. Sorting (σ) showed the highest value during 2004 at 3C (1.2) and lowest during 2006 at 2C (0.3). Skewness was the most variable parameter, both in time and space, reaching a high of 1.99 (2004) and a low of 0.34 (2006) at 3L. The organic carbon showed its minimum value (0.0) at 3C, 5L and 5C during 2006. The lowest value of $CaCO_3$ was at 3L in 2006 (0.1) (Table 2). Significant differences in environmental parameters were measured amongst years, by the PERMANOVA test ('2004' vs '2006': $t = 2.4$ $P < 0.01$; '2003' vs '2006': $t = 2.2$ $P < 0.01$; '2005' vs '2006': $t = 1.7$ $P < 0.05$). These differences were due to great variation in grain size parameters (i.e., Mz, Sk, Kg) and $CaCO_3$ amongst years ($H = 10.78$ $P < 0.01$; $H = 11.83$ $P < 0.01$; Kg = 22.67 $P < 0.01$; $H = 8.40$ $P < 0.05$). No statistical

Table 2 Abiotic, biotic parameters and functional indices: grain size (%), grain size parameters (Mz. Mo, σ, Sk, Kg), percentage of organic carbon (Corg), percentage of calcium carbonate (g), diversity indices (S, d, J′, H), (Fdis) and Fdis/H′, for each site

Stations	Pebble	Gravel	Sand	Silt	Mz	Mo	σ	Sk	Kg
1L03	0.0	0.0	100.0	0.0	1.8	2.0	0.7	1.0	0.0
1S03	0.0	0.0	100.0	0.0	1.9	2.0	0.6	1.8	0.2
2L03	0.0	0.0	100.0	0.0	2.1	2.0	0.7	1.2	0.2
2S03	0.0	0.0	97.7	2.3	2.1	2.5	0.5	1.3	− 0.1
3L03	0.0	0.0	100.0	0.0	2.0	2.5	1.1	1.1	0.0
3S03	0.0	0.0	100.0	0.0	1.8	2.5	0.8	1.8	− 0.3
4L03	0.0	0.0	100.0	0.0	2.0	2.0	0.5	1.1	0.1
4S03	0.0	4.9	92.7	2.4	2.1	2.5	0.7	1.7	− 0.2
5L03	0.0	0.0	100.0	0.0	1.6	1.5	1.0	1.0	0.3
5S03	0.0	0.0	100.0	0.0	2.3	2.5	0.6	1.3	− 0.1
1L04	0.0	0.0	100.0	0.0	2.6	3.0	0.8	0.9	− 0.2
1S04	0.0	0.0	100.0	0.0	2.0	2.0	0.6	1.6	− 0.1
2L04	0.0	0.0	100.0	0.0	1.7	1.5	1.0	0.9	0.2
2S04	0.0	0.0	100.0	0.0	2.0	2.5	0.5	1.1	− 0.2
3L04	0.0	0.0	100.0	0.0	2.0	2.5	1.2	0.9	− 0.2
3S04	0.0	0.0	100.0	0.0	1.8	2.0	0.6	2.0	0.1
4L04	0.0	0.0	97.7	2.3	2.1	2.0	0.6	1.1	0.2
4S04	0.0	0.0	100.0	0.0	2.0	2.5	0.5	1.0	− 0.2
5L04	0.0	0.0	100.0	0.0	1.8	2.0	0.7	1.0	0.0
5S04	0.0	0.0	100.0	0.0	1.9	2.0	0.5	1.9	0.2
1L05	0.0	0.0	100.0	0.0	2.0	2.0	0.7	1.6	0.1
1S05	0.0	0.0	100.0	0.0	1.9	2.0	0.5	1.8	0.3
2L05	0.0	0.0	100.0	0.0	1.3	1.5	0.7	1.0	− 0.1
2S05	0.0	0.0	98.1	1.9	1.9	2.0	0.6	1.8	0.2
3L05	0.0	0.0	94.9	5.1	1.9	2.0	1.0	1.6	0.1
3S05	0.0	0.0	100.0	0.0	2.0	20.0	0.5	1.1	− 0.1
4L05	0.0	0.0	100.0	0.0	1.9	2.0	0.6	1.4	− 0.1
4S05	0.0	0.0	100.0	0.0	1.7	2.0	0.6	1.1	0.2
5L05	0.0	0.0	95.6	4.4	2.1	2.5	0.7	1.3	0.1
5S05	2.4	4.9	90.2	2.4	0.6	0.0	1.1	1.0	0.1
1L06	0.0	0.0	100.0	0.0	1.9	2.5	0.6	1.1	1.1
1S06	0.0	0.0	100.0	0.0	1.5	1.5	0.5	1.0	1.0
2L06	0.0	0.0	100.0	0.0	1.5	2.0	0.3	0.7	0.7
2S06	0.0	0.0	97.8	2.2	1.7	2.0	0.5	1.1	1.0
3L06	0.0	0.0	100.0	0.0	1.5	2.0	0.4	0.9	0.9
3S06	0.0	0.0	97.8	2.2	2.0	20.0	0.6	0.3	1.0
4L06	0.0	0.0	100.0	0.0	2.0	2.0	0.5	1.0	1.0
4S06	0.0	0.0	100.0	0.0	1.6	2.0	0.4	1.0	1.0
5L06	4.4	2.2	93.3	0.0	0.7	1.5	1.1	1.3	1.3
5S06	0.0	4.5	95.5	0.0	0.2	− 0.5	0.8	0.7	0.7

Table 2 continued

Stations	$CaCO_3$	Corg	S	d	J′	H′ (log_2)	FDis	FDis/H′
1L03	1.3	0.0	4	1.86	0.96	1.92	3.60	1.87
1S03	1.7	0.1	6	2.28	0.94	2.42	5.30	2.19
2L03	2.7	0.1	3	1.44	0.95	1.50	4.47	2.98
2S03	2.6	0.1	4	1.14	0.71	1.43	3.97	2.78
3L03	2.4	0.1	7	2.16	0.90	2.52	4.82	1.91
3S03	1.5	0.0	5	1.52	0.83	1.92	4.84	2.52
4L03	2.0	0.1	6	1.95	0.85	2.20	3.94	1.79
4S03	2.4	0.0	2	1.44	1.00	1.00	4.19	4.19
5L03	1.2	0.1	6	2.01	0.88	2.28	3.61	1.58
5S03	2.1	0.1	4	1.30	0.88	1.76	4.64	2.63
1L04	3.0	0.1	5	1.92	0.93	2.16	4.99	2.31
1S04	2.0	0.1	4	2.16	1.00	2.00	5.49	2.74
2L04	0.5	0.0	3	0.76	0.46	0.73	1.49	2.03
2S04	2.2	0.1	4	1.25	0.84	1.69	3.09	1.83
3L04	2.0	0.1	9	2.72	0.85	2.69	4.36	1.62
3S04	1.4	0.0	6	1.73	0.81	2.11	3.34	1.59
4L04	2.4	0.1	7	2.27	0.86	2.41	3.72	1.54
4S04	1.9	0.0	7	2.34	0.78	2.19	4.01	1.83
5L04	1.8	0.1	6	2.28	0.94	2.42	4.25	1.75
5S04	1.5	0.0	6	2.57	0.98	2.52	4.66	1.85
1L05	2.1	0.1	7	2.12	0.83	2.34	3.93	1.68
1S05	2.0	0.1	6	1.76	0.78	2.02	3.49	1.73
2L05	0.8	0.0	6	2.09	0.79	2.05	3.52	1.72
2S05	1.4	0.0	3	0.87	0.58	0.92	2.33	2.53
3L05	2.0	0.0	7	2.27	0.89	2.50	4.05	1.62
3S05	2.7	0.1	4	1.86	0.96	1.92	4.62	2.40
4L05	2.6	0.0	7	2.61	0.94	2.65	4.99	1.88
4S05	1.0	0.0	6	2.40	0.97	2.50	4.41	1.77
5L05	2.7	0.1	8	2.42	0.74	2.21	3.91	1.77
5S05	0.7	0.0	3	1.44	0.95	1.50	3.12	2.08
1L06	2.0	0.1	4	1.86	0.96	1.92	3.62	1.88
1S06	0.9	0.0	5	1.48	0.67	1.56	3.76	2.41
2L06	1.0	0.0	1	0.00	nd	0.00	0.00	0.00
2S06	1.2	0.0	5	1.67	0.72	1.67	3.79	2.26
3L06	0.9	0.0	6	1.85	0.92	2.37	5.69	2.41
3S06	2.0	0.1	2	1.44	1.00	1.00	3.76	3.76
4L06	2.0	0.1	2	1.44	1.00	1.00	4.54	4.54
4S06	0.8	0.1	3	1.12	0.79	1.25	3.74	2.99
5L06	0.6	0.0	9	2.95	0.86	2.74	5.27	1.92
5S06	0.1	0.0	6	2.79	1.00	2.58	5.19	2.01

Mz mean grain size, *Mo* mode, σ grading, *Sk* skewness, *Kg* kurtosis, *S* number of species, *d* Margalef's richness, *J′* Pielou's evenness, *H′* Shannon 's diversity, *Fdis* functional indices dispersion, *Fdis/H′* functional redundancy

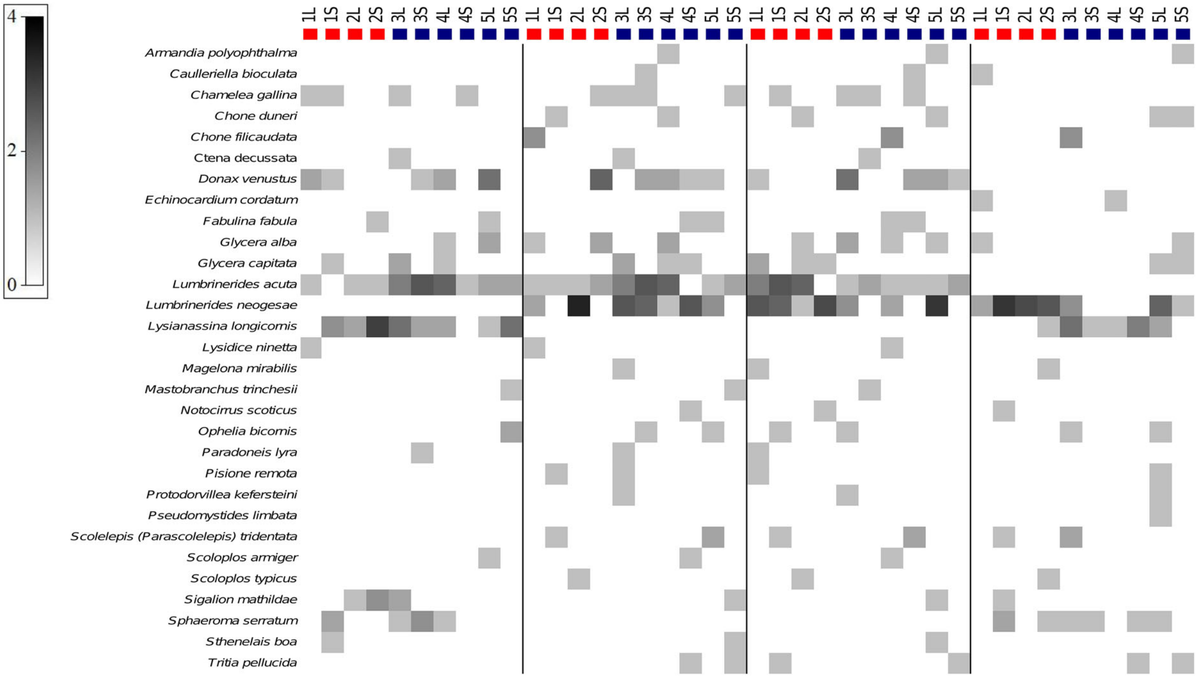

Fig. 2 Shade plot representing the species composition along a temporal scale. Data are previously square root transformed. The stations potentially influenced by the coastal defence are indicated with red squares

differences were measured in physical–chemical parameters amongst transects and sampling positions.

A total of 446 specimens belonging to 37 species were recorded during the 4-year study (Table 2, Fig. 2). The number of species ranged from a minimum of 1 (St. 2C in 2006) to a maximum of 9 (St. 3C and St. 5C in 2004 and 2006, respectively). Overall, the higher number of taxa were noticed at landward stations compared to seaward ones (Mann–Whitney *U* test: $z = 2.0$; $P < 0.05$). The total abundance ranged from 6.6 ind. m^{-2} (4L in 2003, 3L and 4L in 2006) to 63.3 ind. m^{-2} (3C in 2004). Polychaetes were by far the dominant group, reaching 71.1% of the total abundance over the whole study period, followed by molluscs (14.7%), crustaceans (13.7%) and echinoderms (0.5%). The most abundant species was *Lumbrinerides neogesae* Miura, 1981, which arrived in 2004 during *in-operam* phases, showing the highest abundance for all the subsequent samplings, reaching 25% of total abundance.

The PERMANOVA main test performed on macrofaunal community highlighted differences in species composition between sampling periods (pseudo-F = 3.9; $P < 0.01$). In particular, as shown by the PERMANOVA pairwise test, each year significantly differed from the other sampling periods, except for '2004 *vs.* 2005' (*in-operam* phase; Table 3). However, species composition significantly varied between stations directly influenced by barrier placement and those that were not, in 2005 and 2006 ($t = 2.3$ and 2.7; $P < 0.01$, respectively).

By SIMPER analysis (Table 3), the dominance of non-indigenous polychaete *L. neogesae* characterized the differences amongst years with a high contribution percentage (percentage of average contribution = 14.5 ± 0.6). Also, the polychaete *Lumbrinerides acuta* (Verrill, 1875), more abundant during *ante-operam* phase, contributed to dissimilarity between 2003 and 2006 (percentage of average contribution = 14.9). Further, the crustacean *Lysianassina longicornis* (Lucas, 1846), observed with high densities in 2003, along with *L. neogesae*, more dominant in 2005, led to the dissimilarity between *ante-* and *in-operam* phases (*L. neogesae* and *L. longicornis* percentage of average contribution = 14.4% and 13.9%, respectively). *L. longicornis* and the crustacean *Sphaeroma serratum* (Fabricius, 1787) were present during 2003 and reappeared in 2006. In contrast, *L. acuta* and the molluscs *Chamelea gallina* (Linnaeus, 1758), *Ctena decussata* (Costa, 1829) and

Table 3 Species contribution to average dissimilarity and PERMANOVA pairwise tests amongst years (SIMPER analysis cut-off 70%)

Species	2003		2004		2005		2006		2003 vs 2004	2003 vs 2005	2003 vs 2006	2004 vs 2005	2004 vs 2006	2004 vs 2006
	ind. m^{-2}		ind. m^{-2}		ind. m^{-2}		ind. m^{-2}		$t = 2.00$, $P < 0.01$ Av. diss. = 74.93	$t = 1.98$, $P < 0.01$ Av. diss. = 74.44	t = 2.53, p < 0.01 Av. diss. = 84.38	Pairwise test: n.s Av. diss. = 62.64	t = 1.98, p < 0.01 Av. diss. = 84.81	t = 2.19, p < 0.01 Av. diss. = 82.86
	Av	SD	Av	SD	Av	SD	Av	SD	Contrib%	Contrib%	Contrib%	Contrib%	Contrib%	Contrib%
Chamelea gallina	1.33	1.63	1.33	1.63	1.33	1.63	0	0	4.93	5.07	4.89	5.34	3.69	4.04
Chone duneri	0	0	0.67	1.33	0.67	1.33	0.67	1.33	–	–	–	3.58	3.14	2.78
Chone filicaudata	0	0	1	3	1	3	1	3	–	–	–	3.53	–	–
Donax venustus	3.67	5.04	4	5.93	3.67	5.04	0	0	8.45	8.23	7.04	9.34	6.91	6.72
Fabulina fabula	0.67	1.33	0.67	1.33	0.67	1.33	0	0	3.07	3.15		3.49	–	–
Glycera alba	1	2.13	1.67	2.69	1.67	2.24	0.67	1.33	4.8	4.8	3.63	6.13	4.61	4.47
Glyceracapitata	1.33	2.21	1.33	2.21	1.33	2.21	0.67	1.33	4.35	4.77	3.82	5.16	3.51	4.01
Lumbrinerides acuta	8.33	7.49	8.33	7.49	8.33	7.49	0	0	7.52	8.15	14.65	8.79	13.38	13.79
Lumbrinerides neogesae	0	0	12.67	12.81	12.33	11.84	12.33	11.84	14.75	14.37	14.91	15.37	13.75	13.6
Lysianassina longicornis	9.67	8.75	0	0	0	0	4.67	5.62	13.64	13.91	11.73	–	8.34	8.49
Ophelia bicornis	0.67	2	0.67	1.33	0.67	1.33	0.67	1.33	–	–	–	3.3	–	–
Scolelepis tridentata	0	0	1	2.13	1	2.13	1	2.13	–	–	–	4.6	3.9	3.53
Sigalion mathildae	2	3.4	0.33	1	0.33	1	0.33	1	4.48	4.45	4.7	–	–	–
Sphaeroma serratum	2.33	3.35	0	0	0	0	2.33	2.13	4.5	4.57	7.01	5.87	5.97	–
Tritia pellucida	0	0	0.67	1.33	0.67	1.33	0.67	1.33	–	–	–	3.74	3.18	3.47

Av. average abundance, *SD* standard deviation, *Contrib%* species contribution to average dissimilarities between groups, *n.s.* no significant

Donax venustus Poli, 1795 were slightly abundant during *ante-* and *in-operam* phases but disappeared *post-operam*. Furthermore, the polychaetes *L. neogesae* and *Armandia polyophthalma (*Kükenthal, 1887) and the mollusc *Tritia pellucida* (Risso, 1826) were absent during the first year and then appeared and dominated (above all *L. neogesae*) during 2004–2005 and 2006.

The Distance-based Linear Modelling (DistLM) applied to the macrofaunal community in the whole study area and periods ($R^2 = 0.14$) indicated organic carbon as the main driver of the species assemblages (Pseudo-F = 2.30; $P < 0.05$).

Diversities and functional features

As regarding the diversity indices, the values of d and H' showed significant differences amongst transects (Kruskal Wallis *H* test = 12.2 and 12.0, $P < 0.05$, respectively). In particular, throughout the whole study period, major values of *d* and *H′* were noticed at transect 'five' compared to transect 'two', as corroborated by *H* test ('five' *vs* 'two': $z = 3.3$ and 3.2, $P < 0.05$, respectively) (Table 2). However, in the whole study area, higher values of richness and diversity were noticed in 2004 and 2005 compared to 2003 and 2006 (Fig. 3a and b).

FDis values varied from a minimum of 0.0 at 2L in 2006 (only one species was observed) to a maximum of 5.7 at 3L in 2006. Overall, FDis values (Fig. 4c) remained stable for most of the study period (FDis average for 2003–2005: 4.0 ± 1.0). Moreover, no differences in functional diversity values were noticed amongst transects and station locations (landward and seaward). In contrast, functional redundancy (FDis/H′) significantly differed amongst years ($H = 8.0, P < 0.05$) and between station positions (*U* test, $z = -2.5$; $P < 0.01$). Higher values of FDis/H′ were observed at stations located seaward during 2006 in particular. As FDis, functional redundancy in the last sampling period showed great variability amongst transects (Fig. 4d). The lower values were observed at stations influenced by the costal defence (FDis/H′ average for transect 'one' and 'two': 1.6 ± 1.1) whereas the higher values were in the other transects (FDis/H′ average for transect 'three', 'four' and 'five': 2.9 ± 1.0).

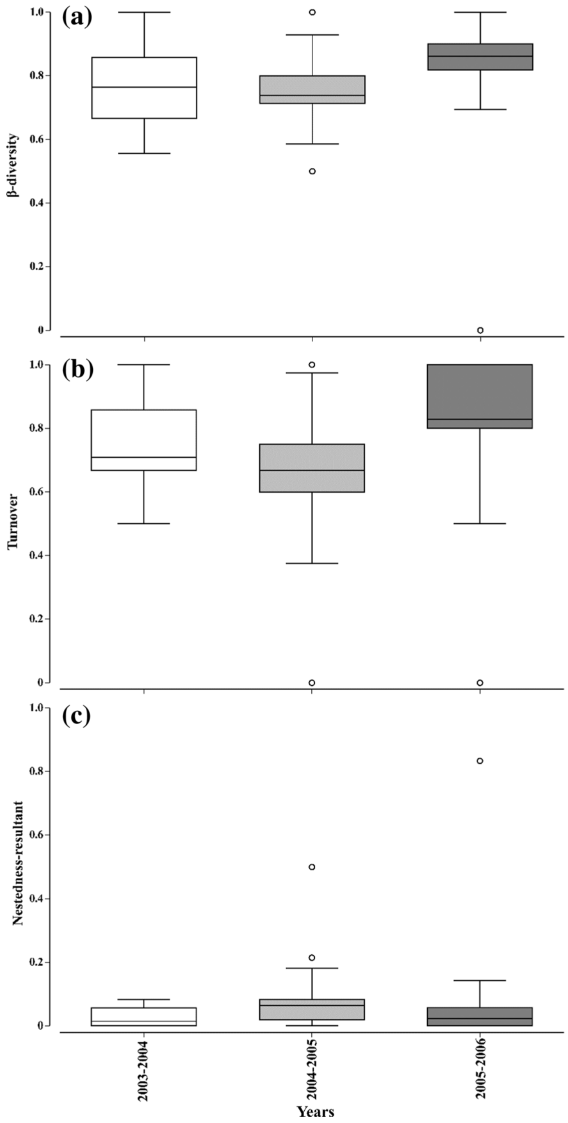

Fig. 3 Boxplots showing the variability of *β*-diversity (**a**) and its components: turnover (**b**) and nestedness-resultant (**c**) of macrofaunal community between 2003–2004, 2004–2005 and 2005–2006

For the entire sampling area and periods, the taxonomic β-diversity was driven more by the replacement of species amongst years than by the presence of a subset of species, except for 2L, in which the β-diversity of community collected between 2004–2005 and 2005–2006 was characterized by high nestedness components (0.50 and 0.8, respectively). Overall, increasing values of β-diversity toward the end of the study period, due to higher values of turnover, were noticed (Fig. 3a–c).

The CWM values for the entire study area and periods showed higher occurrences (CWM values > 2.5) of the following categories: *gonochoric*,

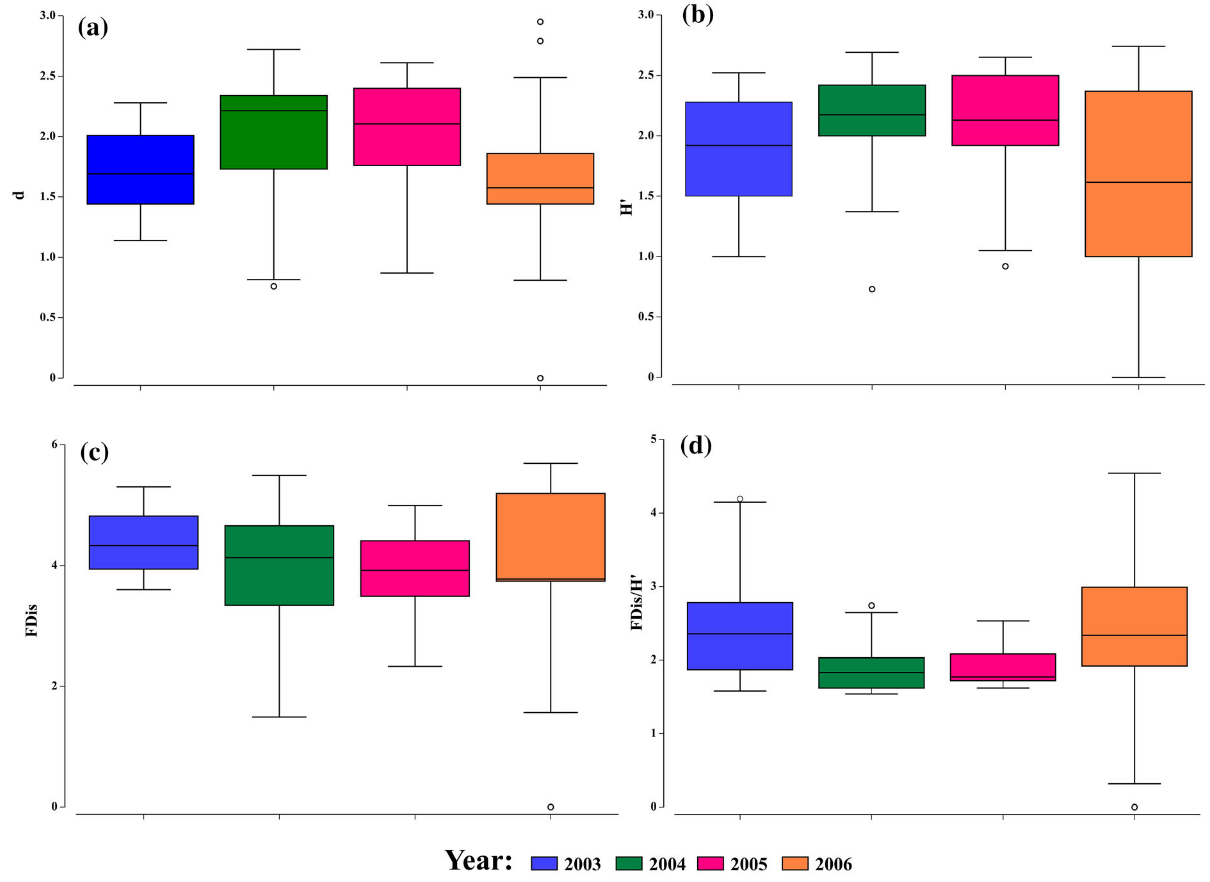

Fig. 4 Variability of richness-d (**a**), diversity-H' (**b**), Functional dispersion-FDis (**c**) and Functional redundancy- FDis/H' (**d**) values of macrofaunal community amongst years

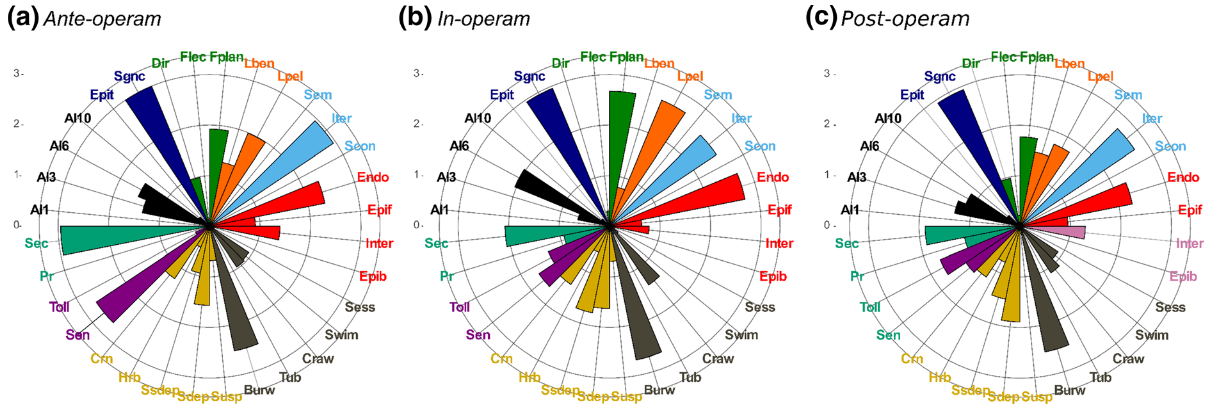

Fig. 5 Community-weighted means of trait category expression (CWM), average values for sampling stations during *ante-* (**a**), *in-* (**b**) and *post-operam* phases (**c**). Colour codes and individual bars represent trait affiliation and trait category expression, respectively (for labels see Table 1)

planktotrophic larvae, *iteroparous*, *suspension feeder*, *burrower and endofauna.* In contrast, less represented categories of traits (CWM values < 0.05) were *adult longevity ≤ 1 year, epitoky, semi-continuous* and *sessile.* The polar plots showed a great variation in certain modalities amongst different phases of barrier placement. Higher occurrences of *adult longevity 3–6 years* and *planktotrophic larvae* with *plankton development* were noticed during the *in-operam* phase compared to the *ante*- and *post-operam* ones whereas increasing CWM values of *sub-surface deposit feeder* were observed at the *post-operam* phase. *Secondary* colonizers and *sensitive* species dominated in 2003, slightly decreasing toward the last part of the study period when increasing occurrences of *tolerant* and *pioneer* modalities were noticed. Since no species were *asex* or *hermaphrodite,* these traits were deleted from the subsequent analyses.

The PERMANOVA main test performed on macrofaunal functional features highlighted differences amongst years (Pseudo-F: 3.6; $P < 0.01$). All sampling years significantly varied between each other, except for ‘2004 *vs* 2005’. In particular, higher values of t-test (PERMANOVA pairwise test) were calculated between ‘2003 *vs* 2004’ and ‘2003 *vs* 2005’ (t = 2.6 and 2.7; $P < 0.01$, respectively). The PERMANOVA two-way (‘years’ × ‘artificial barrier’) highlighted significant differences amongst stations influenced by the coastal defence and sampling years (Pseudo-F: 3.3; $P < 0.01$). In particular, in 2006 the traits occurrences significantly varied amongst the stations influenced by the coastal defence and the ones that were not (t = 2.6; $P < 0.01$). In addition, any differences were noticed amongst transects and between stations positions (i.e., land- and seaward). The DistLM applied to CWM values did not highlight any environmental drivers of traits occurrences.

The Principal Coordinates Analyses (PCoA) were carried out on traits-categories and accounted for 71.3% of the total variation (PCo1: 49.1% and PCo2: 22.2%). In Fig. 6, we overlaid the trait categories that significantly differed amongst years, highlighted by the Kruskal–Wallis test (Table 4). The modalities *benthic larvae, interface, direct development, swimmer, adult longevity 1–3 years, secondary colonizer and sensitive* were the predominant element of the positive part of PCo1, due to their higher occurrences at sampling stations in 2003 and stations of transects ‘three’ and’four’ in 2006. The sampling stations in 2004 and 2005 were plotted on the left-hand side of the ordination (negative part of PCo1), due to the high occurrences of categories such as *pioneer*, *sub-surface deposit feeder*, *adult longevity 3–6 years*, *endofauna and pelagic larvae*. In contrast, the trait category *tolerant* was the predominant element of the second axis, mainly expressed at stations collected in 2006,

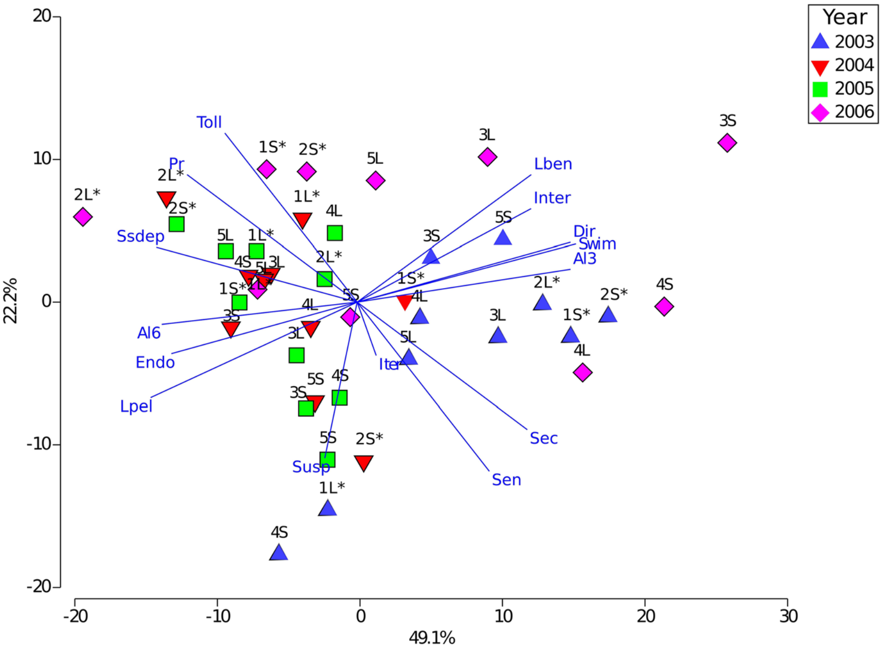

Fig. 6 PCo ordination of trait categories occurrences (CWM values) of sampling stations and periods. Modalities that significantly differed amongst years were overlaid (blue arrows). Years are indicated with different colours and shapes. The asterisk refers to stations nearby the coastal barrier

Table 4 Modalities significantly differed amongst years by Kruskal–Wallis test (main and pairwise tests)

Trait categories	Main test (H)	P value	Post hoc
Adult longevity 1–3 yrs (Al3)	10.15	< 0.05	
Adult longevity 3–6 yrs (Al6)	10.12	< 0.05	
Direct development (Dir)	13.75	< 0.05	2003 vs 2004’, $z = 3.00$, $P < 0.05$; ’2003 vs 2005’ $z = 2.98$, $P < 0.05$
Benthic larvae (Lben)	8.44	< 0.05	
Pelagic (Lpel)	10.72	< 0.05	
Iteroparus (Iter)	10.57	< 0.05	2003 vs 2005’ $z = 3.00$, $P < 0.05$
Sensitive (Sen)	14.5	< 0.01	2003 vs 2004’, $z = 2.78$, $P < 0.05$; ’2003 vs 2004’ $z = 2.81$, $P < 0.05$; ’2003 vs 2006’ $z = 3.50$, $P < 0.01$
Tolerant (Toll)	14.5	< 0.01	2003 vs 2004’, $z = 2.78$, $P < 0.05$; ’2003 vs 2004’ $z = 2.81$, $P < 0.05$; ’2003 vs 2006’ $z = 3.50$, $P < 0.01$
Pioneer (Pr)	12.72	< 0.01	2003 vs 2004’, $z = 2.78$, $P < 0.05$; ’2003 vs 2004’ $z = 2.82$, $P < 0.05$; ’2003 vs 2006’ $z = 3.50$, $P < 0.01$
Secondary (Sec)	12.72	< 0.01	2003 vs 2004’, $z = 2.73$, $P < 0.05$; ’2003 vs 2004’ $z = 2.92$, $P < 0.05$; ’2003 vs 2006’ $z = 2.87$, $P < 0.01$
Suspension feeder (Susp)	9.58	< 0.05	2004 vs 2006’, $z = 2.66$, $P < 0.05$
Sub-surface deposit feeder (Ssdf)	8.17	< 0.05	
Interface (Inter)	8.95	< 0.05	
Endofauna (Endo)	9.44	< 0.05	
Swimmer (Swim)	11.22	< 0.05	

n.a. not available

influenced by the artificial barrier. In the negative part of PCo2, *suspension feeder* characterized the landward stations of transects not influenced by the coastal defence in 2004 and 2005 and 1C in 2003.

Discussion

The use of artificial barriers to mitigate coastal erosion is common worldwide (Firth et al., 2016). As a result, understanding what happens in the ecosystem following this type of anthropic intervention is an essential issue for the management of the coastal zone. In this view, the analysis of functional traits here conducted allows for more in-depth investigation of the responses of the ecosystem to natural and anthropic disturbance (Munari, 2013; Nasi et al., 2018; D’Alessandro et al., 2020). In this paper, we explored biodiversity and functional attributes of soft-sediment invertebrate assemblages influenced by barrier placement along a temporal scale, assessing in particular the plasticity of the macrofaunal community and thus its ability to adapt after a disturbance event.

Environment and communities answers

The grain size sediments of our study are characterized by a very high percentage of sand, evenly distributed in the whole area of study. This homogeneity agrees with previous studies conducted in the Gulf of Milazzo that reported substantial medium-fine sedimentology of the eastern part, in contrast to the western part characterized by biogenic and terrigenous sediments (D’Alessandro et al., 2014; D’Alessandro et al., 2016). This feature is also confirmed by grain size statistic parameters that, over the years, showed a slight increase of grain size and of sorting (Kulkarni et al., 2015). In addition, the high positive correlations found between organic carbon content (Mz [Φ]) and carbonate fraction (gr of CaCO3), the latter of which is of biogenic origin, showed as a faint increase in sediment grain size corresponding to a decreasing organic matter availability and bioclastic deposition. This paucity of organic content could in addition be ascribed to the shallow environment severely influenced by waves and currents, along with coarse grain size, which reduces the vertical and lateral deposition and accumulation of organic matter particles (Donald & Larry, 1982).

Regarding the macrofaunal investigation, the community recorded can be ascribed to the "Well Sorted Fine Sands Biocenosis (WSFS)", corresponding to the SFBC (Sables Fins Bien Calibrés) biocenosis of Pérès (1967) and to the "sandy deep bottom community", 3–30 m depth, of Ros et al. (1985). These WSFS communities, as confirmed by our results, are notoriously subject to space-temporal changes due to a combination of hydrodynamic forcing and anthropogenic pressures (e.g., the embankment of terrestrial lands, dike construction, dredging and recharging of beaches; Dauvin et al., 2017). Moreover, the marked variability of species composition that we observed amongst 4 years, between *ante-* and *post-operam* phases, also agrees with such known changeability. An example is given by two molluscs *T. pellucida* and *D. venustus* belonging to SFHN ("fine sands in the shallow water of the surf zone"; Pérès, 1967). Indeed, in *ante-operam* of barrier placement, the community was characterized by both of these species, which endorsed the higher hydrodynamic conditions (Febvre-Chevalier, 1969). However, in 2006 we noticed a disappearance of *D. venustus* in all sampling stations, whereas *T. pellucida* was completely absent at stations near the barrier. The oligotrophic shallower WSFS communities are notoriously subject to space-temporal changes due to a combination of hydrodynamic forcing and anthropogenic pressures enhancing the vulnerability of benthic habitats. This aspect is mirrored in the settlement of NIS species toward the end of the study period: the polychaete *L. neogesae*, introduced by shipping in the Mediterranean at the time of our investigation (Gravina & Cantone, 1991; Servello et al., 2019) replaced the co-generic *L. acuta* dominant at *ante-operam* phase. Despite the variation of species amongst years, we also noticed a return of certain species. The crustaceans *L. longicornis* and *S. serratum,* promptly reappearing in the area *post-operam*, showed greater resilience compared to other species that disappeared in 2006 (the bivalves *D. venustus* and *T. pellucida*) (Fig. 2). This shift in species composition, at last, resulted in a partial change and re-organization of the primitive community, driven by the *post-operam* changed seafloor morphology and sedimentation rate. Indeed, the WSFS confirmed to be "a resistant and resilient marine habitat under diverse human pressures" (Dauvin et al., 2017). These results further confirm the influence of barrier placement on the macrofaunal community and on sea bottom hydrodynamics, reducing energy.

Biodiversity and functional indices

Lower diversity values at stations directly influenced by barrier placement were observed. These results were according to several studies, which testified relationships between biodiversity loss and human-induced disturbances (Chapin et al., 2000; Elahi et al., 2015; D'Alessandro et al., 2020). In particular, the biodiversity increase observed during the *in-operam* phase agrees with the intermediate disturbance theory of Connel (1978), which relates diversity peaks to the trade-off between competitive and colonizing abilities to settle species. Persisting through the disturbance, some species that better weather the environmental variation maintain their population size at the expense of competitors (Nasi et al., 2017). This latter aspect was mirrored in 2006 (*post-operam* phase), when a decreasing number of species and biodiversity were observed. We inferred that the NIS *L. neogesae*, initially favoured as a tolerant and pioneer species, later stabilized its dominant role in the benthic community as a superior competitor in the new ecological context. The observed positive covariance between environmental changes (variation in hydrodynamic regime and sedimentation rates) and competition is highlighted. Covariance, indeed, is based on species-specific responses to the environment and is mainly density-dependent (Yuan & Chesson, 2015). This effect occurs when a species (in our case *L. neogesae*) reaches high density, and consequently becomes an even more able competitor. In addition, the β-diversity highlighted a large turnover of species that especially concerned the 2003–2004 to 2005–2006 transition. By the components partitioning of the β-diversity, the turnover of species resulted higher than nestedness, as shown at sites with smaller numbers of species, where the biotas are not subsets of the richer sites (Baselga, 2012) but the establishment of new species. Therefore, in Villafranca seafloors, the positioning of the barrier has generally originated a spatial turnover of species, implying the replacement of some species by others leading to a great change of the community from *ante-operam* to *post-operam* phases (Baselga, 2012). The sole exception was found in the station 2L, landward in the proximity of barriers, during *in-* and *post-operam* phases (see Fig. 3). The β-diversity of the 2L community resulted in a strict subset (i.e., high values of nestedness), tied to the dominant role of the NIS. These results were mirrored as well in the lowest FDis values observed at stations belonging to transect 2 and for the remaining years. Indeed, the presence of few species and the high dominance of the NIS radically reduced the functional diversity at 2L and 2C (Laliberté & Legendre, 2010).

Overall, the functional diversity did not highlight any pattern with biodiversity, so the coastal defence did not seem to affect the functional diversity of the macrofaunal community (see Fig. 4). The perceived stability of functional features could be linked to functional redundancy of the macrofaunal assemblage, where higher species richness was not associated with higher FDis (Cadotte et al., 2011). In our case study, generally lower values of functional redundancy (FDis/H') were noticed during *in-operam* phase compared to *ante–* and *post-operam* ones. However, despite the great turnover of species and variation in community composition, few functional changes affected the macrobenthic community. Such functional homeostasis agrees with the redundancy hypothesis, according to which if multiple species perform the same function and thus express similar trait values, in the case of one being eliminated, others remain to continue or potentially even increase functioning (Yachi & Loreau, 1999). In *ante*-and *post-operam* phases, at stations near coastal defence, the community displayed lower redundancy, with species strictly performing specific functions. However, after the barrier placement, those stations showed low functional diversity, with a minor overlapping of functional niches amongst species, resulting in these sites being more susceptible to species loss and function than others (Gamfeldt et al., 2008).

Macrofaunal functional changes

The functional identity, similar to macrofaunal structural analysis, showed significant differences amongst sampling periods. Specifically, functional occurrences varied between *ante-* and *in–operam* phases, the latter showing a larger dominance of species with adult longevity 3–6 years and planktotrophic larvae over species with other life-cycle properties (e.g., direct or benthic development). Larval development is known to reflect species adaptation to environmental variability (Munari, 2013), providing species with planktonic-planktotrophic larval development a greater dispersal potential and a lower risk of extinction than in organisms with other types of development (Marshall and Alvarez-Noriega, 2020). In our case study, the dominance of species with planktonic-planktotrophic larvae is a clear response to the high environmental variability following the barrier placement. The incising of this type of larval feeding type followed the pattern of pioneer and tolerant traits, whose higher occurrences were noticed during the *in-operam* phase. In fact, pioneers are species that possess life-history characteristics (e.g., planktotrophic larval development) that allow them to respond quickly to disturbances (Norkko et al., 2006). Therefore, we can infer that during 2003, the community was dominated by sensitive and secondary colonizer species, whereas in 2004 and 2005, tolerant and pioneer modalities prevailed. Results also suggested that the prevalence of key species sensitive to a stressor may have affected native community resilience. It is known that the presence of species that exhibit sensitivity to environmental or anthropogenic stressors may lead to local regime shifts throughout, i.e., major changes in species composition and function (Thrush et al. 2009). This trend agrees with that reported by Gómez, Gesteira and Dauvin (2005) in which, in response to spilled oil, the macrofaunal community displayed an initial proliferation of the more resistant species whilst the last phase was characterized by a new functional structure.

However, a slight variation of functional occurrences both in sampling areas and periods suggests that, despite the changes in community composition due to the drastic reduction of sensitive species, the presence of pioneer and tolerant species might avoid the loss of function. The role of pioneer species, able to proliferate in disturbed habitats due to their ability to mediate the benthic communities' re-organization (Wali, 1999), may have reduced the disturbance effects, conferring resilience to the community (Thrush et al., 2009). Even if the macrofaunal community as a whole exhibited a certain degree of resilience, a variation was observed in feeding modalities at stations directly influenced by the artificial structure during the *post-operam* phase. In 2003, at stations near coastal defence, higher occurrences of suspension feeders resulted, if compared to 2006 where this modality was completely absent (see Fig. 5). Similar results were obtained by Munari (2013), in the Northern Adriatic Sea, in which the authors observed a decreasing number of suspension feeder modalities near the artificial barrier due to unfavourable conditions. In our case study, the decrease of suspension was coupled with a major increase of sub-surface deposit feeders due to the dominance of NIS *L. neogesae*. This species, as most *Lumbrineridae*, is a non-selective burrow sub-surface deposit feeder, which obtains food from deeper sediment layers by eating particles incorporated into a mucous burrow (Jumars et al., 2015a, b), contributing to the particles' transport within sediments by enhancing the benthos elemental cycling (Törnroos & Bonsdorff, 2012). However, the functions of suspension feeders were not lost but changed by those of surface deposit feeders. The latter feed from the surface of the substratum enhancing the elemental cycling within benthos and within the water column (Newell, 2004). Lastly, we can argue that *L. neogesae*, being a non-indigenous species, supplanted native taxa, influencing the entire structure of the macrofaunal community. However, this species contributed to functional adjustments in the community influenced by disturbances preventing the loss of ecosystem functions.

Conclusion

In this 4-year study period, we highlighted a direct influence of artificial coastal barriers on the surrounding environment, with the consequent variation in macrofaunal biodiversity, species composition and traits occurrences. The effects of a disturbance generated by human activity further confirm it to be a key factor in determining the success of opportunistic and invasive species in marine systems at the expense of pre-existent species. Nevertheless, the resilient shallow-water communities may respond to disturbances with a rapid structural and functional adjustment, performing for the ecosystem the same properties as before. Since the use of artificial barriers to mitigate coastal erosion is widespread, understanding what happens in the ecosystem following this type of anthropic intervention is an essential issue for the management of the coastal zone. Our findings indicate that by combining the classic taxonomic approach, which considers the structural characteristics of the macrofaunal community, with a novel approach based on turnover biodiversity and the functional attributes of invertebrates, more insight into how the community copes with changes or a disturbance event could be gained. Therefore, these combined approaches in coastal management can be useful in mitigating the negative impacts of human activities and enhance their contribution to marine biodiversity and ecosystem functioning.

Acknowledgments The authors thank the Villafranca Tirrena municipality for their support during the investigations.

Author contributions GS designed methodology, and collected the data; MD, FN, LF analysed the data; MD, FN and GS led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

Funding No funds, grants, or other support was received.

Data availability All data are included in both the text and supplementary material.

Declarations

Conflict of interest This work does not present potential conflicts of interest with other authors, research groups, and public or private agencies.

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