Research Article

Biodiversity, feeding habits and reproductive strategies of benthic macrofauna in a protected area of the northern Adriatic Sea: a three-year study

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Abstract

The macrozoobenthic community at a sublittoral station located in the Marine Protected Area of Miramare, Gulf of Trieste (Italy) was investigated monthly from June 2002 to July 2005. Community variables were studied and related to food sources (particulate, total and biopolymeric carbon contents, benthic microalgae and meiofauna). In addition, macrofaunal response to a heatwave that occurred in summer 2003 in the area was also explored. Univariate and multivariate analyses highlighted that the macrozoobenthic community structure shifted towards the end of the study. Diversity remained fairly stable throughout the study, despite the high turnover values. From a dominance of short-lived invertebrates related to irregular fresh organic matter inputs, the community shifted toward long-lived taxa, principally related to an increase of biopolymeric C and microalgal biomass. Semelparous invertebrates seem to be less resistant to high temperatures compared to iteroparous ones. The latter proved to be capable competitors since they prevailed over the semelparous species towards the end of the study.

The community exhibited a certain degree of resistance to high temperature, due to the adaptation of the macrofaunal invertebrates to this particular stress, induced by the wide natural fluctuations in temperature that occur on a seasonal basis in the Gulf of Trieste. This study highlights the importance of long datasets to assess the state and ecological processes of macrofaunal communities.

Keywords: Soft bottom macrozoobenthos, Community structure, Feeding habits, Reproductive strategies, Environmental factors, Northern Adriatic Sea.

Abbreviations

POC particulate organic carbon
TOC total organic carbon
BPC biopolymeric carbon
MPBB microalgal biomass
Meio meiofauna
SDF surface deposit feeders
SSDF subsurface deposit feeders
SF suspension feeders
P predators
OMN omnivores
G grazers
I iteroparous
S semelparous
C semi-continues

Introduction

Coastal benthic macrofaunal communities are subjected to fluctuations in response to natural environmental drivers and anthropogenic pressures, which vary in frequency and intensity, both on a temporal and spatial scale (Boero, 1994; Turner *et al.*, 1995). As a consequence, the structure (i.e. abundance, biodiversity, species composition) of these communities is constantly changing, hence reducing their stability. Stability *per se* is not a simple characteristic of a community, but rather a multiplicity of distinct attributes (Putman & Wratten, 1984): persistence, variability, resilience and resistance. Persistence can be defined as the constancy in some parameter (e.g. number of species, taxonomic composition, size of a population) of the system over time; variability is the degree to which a parameter fluctuates over time; resilience refers to the ability of a system to recover and continue functioning after disturbance; and resistance describes the ability of the system to withstand or resist such perturbation in the first place (Turner *et al.*, 1995 and references therein). The changes in community structure are primarily influenced by seasonality (Marchini *et al.*, 2004; Quijón *et al.*, 2008) altering seawater temperature, primary production and food availability. Besides the predictable cycle of

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seasonality, shallow coastal water sedimentary macrobenthos shows year-to-year variability (Warwick *et al.*, 2002). Unpredictability of weather conditions (e.g. cold winters and heavy storms), variations in current direction or velocity, flood and drought events, and unusually high temperature are physical-chemical processes that can cause shifts in community stability (Hermand *et al.*, 2008; Munari, 2011; Somerfield *et al.*, 2014). In addition to these physical variations, biological variability such as year-to-year differences in seasonal reproduction and recruitment, predation, species dominance, competition for food and space or inhibition of recruitment (Giangrande *et al.,* 1994; Rossi, 2003; Reiss & Kröncke, 2005; Quijón & Snelgrove, 2005) can be responsible for high variability within the faunal assemblage. The detection of changes in specific drivers is of primary importance because they often alter the conditions of the system (especially food sources) in an apparently unpredictable way. Food supply is a key factor structuring marine zoobenthic communities in terms of functional aspects of biodiversity, namely feeding habits and reproductive strategies. The organic material that benthos receives can have different effects depending on the concentration and timing of delivery (Widdicombe & Austen, 2001). The food supply to benthic organisms relies on the sedimentation of organic matter that is produced in the euphotic zone by primary producers. Particulate food is supplied to the seafloor by either horizontal transport of phytodetritus from terrestrial or vertical transfer of marine planktonic production (Desrosiers *et al.*, 2000). In the Mediterranean, the most important energy input to the benthos occurs shortly after the spring and autumn blooms, which take only a few days to create a tight coupling between the pelagic and benthic system (Coma *et al.*, 2000; Cibic *et al*., 2007b). The phytoplankton pulses of organic matter thus constitute labile directly available and highly nutritive food sources for macrofaunal communities (Quijón *et al.*, 2008 and reference therein). Also, benthic microalgal organisms are preferred high-quality food sources for many soft-bottom benthic invertebrates, deposit feeders in particular, due to a well-balanced content of essential fatty acids and amino acids (Sköld & Gunnarsson, 1996; Hardison *et al.*, 2013). Both benthic microalgae and meiofauna represent a basic food source for macrofaunal invertebrates (Van Colen *et al.*, 2015).

The importance of changes in shallow macrobenthic communities in relation to environmental factors and food source supplies has been extensively studied over the past twenty years, both in field studies on spatial scales (Turner *et al.,* 1995; Simonini *et al.*, 2004; Occhipinti-Ambrogi *et al.*, 2005; Hermand *et al.,* 2008) and in experimental ones (Bolam & Fernandes, 2002; Rossi 2003; Levinton & Kelaher, 2004). However, the role of the food supply in structuring the community along a temporal scale has received less attention. The study of the macrofaunal community and its trophic interactions with other benthic communities (i.e. microalgal and meiofaunal organisms) can be clarified by using functional traits analysis. Functional traits, in particular feeding habits and reproductive frequencies, reflect the components of functioning and are used as proxies for ecological processes such as their role in the trophic pathways and community development along the temporal scale (Törnroos & Bonsdorff, 2012).

Macrofaunal community dynamics in relation to environmental parameters are less known in the Adriatic Sea, especially in its north-western part. Indeed, to date most of the literature on the Gulf of Trieste has investigated macrozoobenthic communities in relation to other aspects: hypoxia and anoxia events that occurred in the 1980s and 1990s (Brizzi *et al.*, 1994; Aleffi *et al.*, 1992; Orel *et al.*, 1993); anthropogenic pressures (industrial activities and sewage outfalls) (Solis-Weiss *et al.,* 2004; Solis-Weiss *et al.*, 2007; Cibic *et al.*, 2008); biodeposition from mussel farms (Aleffi *et al.*, 2006), and riverine inputs (Faresi *et al*., 2012). In contrast, the role of the food supply in structuring the macrofaunal community has not been considered yet.

Here we present the main results obtained over a three-year study of structural macrofaunal community changes (abundance, biodiversity, community composition, feeding habits and reproductive frequencies) in relation to environmental fluctuations (temperature and dissolved oxygen concentration) and food sources (organic matter from the water column and surface sediments, benthic microalgal biomass and meiofauna abundance) in a sublittoral site in the northern Adriatic Sea.

The choice of the site, a virtually pristine area (the Marine Protected Area of Miramare), was driven by the need to attribute the observed response solely to natural temporal variability without any evident anthropogenic disturbance.

More precisely, the aim of this study was to answer the following questions: 1) How stable is the macrofaunal community over time? 2) Are the feeding habits and reproductive frequencies of the macrobenthic community related to the food supply? 3) Is the resistance or resilience of the macrofaunal community a consequence of the observed environmental variations over the three-year study period?

Materials and Methods

Study site

The Gulf of Trieste, located at the north-western end of the Adriatic Sea, is a shallow basin of about 600 km² with a coastline of about 100 km. It is connected to the rest of the Adriatic Sea by a sill (≈ 22 m depth) located in the southern part of the basin (Ogorelec *et al.*, 1991). The Gulf experiences annual fluctuations of temperature varying from 5°C to > 24°C at the surface and from 6 °C to >20°C at the bottom. The general pattern of currents in the

Gulf may be rapidly modified in response to intense local atmospheric forcing (winds) and river plume (Querin *et al.*, 2007; Malačič & Petelin, 2009). The region is highly influenced by the Bora, a north-easterly wind characterized by strong intensity that is able to mix the entire water column also due to the shallow depth of the basin (Querin *et al.*, 2007). The dominant sediment type in the Gulf is sandy-mud but the composition of soft bottoms can vary from sands with patches of rocks to detrital mud (Brambati & Catani, 1988). Sedimentation within the Gulf is mainly controlled by river inputs rather than marine currents and the main terrigenous sediments originate from the Isonzo River (Covelli & Fontolan, 1997). The annual average sedimentation rate is about 1 mm y^{-1} in the middle of the Gulf and increases up to 2.5 mm y^{-1} in front of the Isonzo River (Covelli *et al.*, 1999 and references therein).

The study was carried out at a costal station (C1: 45.700830° N, 13.71000° W) (Fig. 1). C1 is located ca. 250 m offshore at a depth of 17 m, within the Marine Reserve of Miramare. This small marine protected area (MPA) is divided into two distinct zones: the inner part (30 ha), subjected to a regime of integral protection, is surrounded by a larger buffer zone (90 ha). Declared an MPA as early as 1979, the Reserve is part of the Natura 2000-network, and represents the only completely protected area in the Italian part of the Gulf of Trieste. At C1, grain size is clayey silt, with <10% sand and organogenic detrital components (Cibic *et al.*, 2007a).

Sampling

Monthly sampling was performed from June 2002 to July 2005. No samples were taken in August and October 2002, October 2004 and February 2005 for logistic reasons.

Sea bottom temperature, salinity and dissolved oxygen concentration were obtained with a CTD probe (Idronaut Ocean Seven 316 and SeaBird 19 Plus).

Water samples for particulate organic carbon were collected with Niskin bottles at 15 m depth.

Sediment samples for the analyses of chemical parameters (total organic carbon, TOC and biopolymeric carbon, BPC) microalgal biomass (MPBB) and meiofaunal abundance (Meio) were collected by a KC Haps bottom corer (KC-Denmark, Silkeborg, Denmark). For the study of Meio, three replicate cores (polycarbonate tubes of 13.3 cm Ø with a sample area of 127 cm^2) were taken down to the depth of 20 cm.

Macrofauna was sampled by collecting three replicates at each sampling occasion using a 0.1 m^2 van Veen grab.

Food sources

Chemical and biological variables were considered as food sources to better understand macrofaunal variations (abundance, biodiversity, community composition, feeding habits and reproductive frequencies) linked to environmental changes (seasonal and year-to-year variations of temperature, dissolved oxygen and organic matter availability). In particular, we considered the following as food sources: particulate organic matter from the water column, total organic carbon in the sediments and especially its labile fraction composed of carbohydrates, proteins and lipids; and finally the microalgal biomass and meiofaunal abundance that were related to the different macrofaunal feeding habits.

Water subsamples for POC analysis of 0.5 l each were filtered through 25 mm Whatman GF/F pre-combusted filters and were stored frozen at -20 °C. The standard
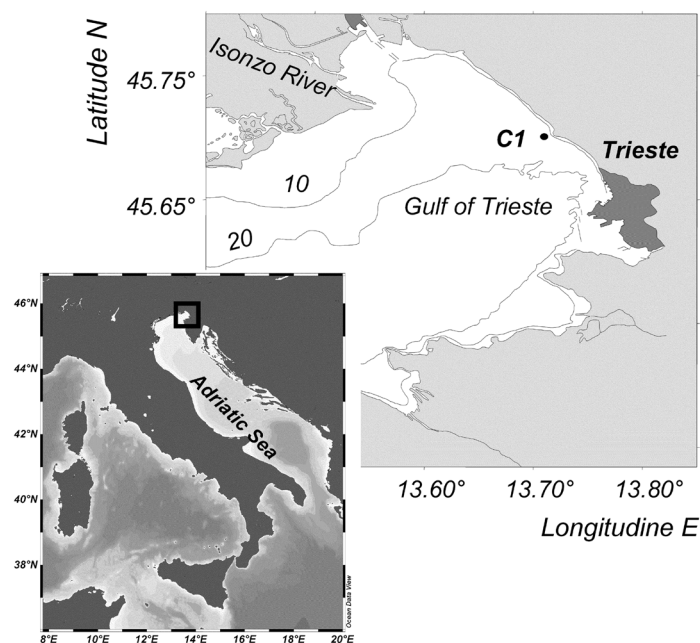

Fig. 1: Location of the study site (45.700830° N, 13.71000° W; 17 m depth) in the coastal area of the Gulf of Trieste.

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POC method was used (Lipizer *et al.*, 2012) and the values were expressed as µmol l^{-1}.

The analyses of TOC and the determination of sediment carbohydrates, lipids, and proteins were performed on subsampled aliquots of oxic sediments as described by Cibic *et al.* (2008). TOC values were expressed as mg g^{-1} dry mass. The sum of carbohydrates, lipids, and proteins carbon was referred to as biopolymeric carbon (BPC) and their values were expressed as µg g^{-1}. The protein-carbohydrate ratio (PTR/CHO ratio) was used to indicate the "age" of the organic matter present in sediments (Pusceddu, 2002).

Microalgal abundance was analysed following the method described by Cibic *et al.* (2007a). Standard deviation of three replicate values was below 25%. MPBB was calculated to assess the carbon content of occurring algae varying in shape and size in accordance with the method proposed by Cibic *et al.* (2007a). MPBB, expressed as mg C cm^{-3}, was obtained by multiplying microalgal abundance (cells cm^{-3}) by the carbon content of each counted cell.

For Meio extraction, sediments were treated according to Cibic *et al.* (2009). The Meio density of the main taxa was expressed as number of individuals per 10 cm^2.

Macrofauna

Sediments were sieved through a 1 mm sieve mesh to retain the fraction of macrozoobenthic organisms. The collected invertebrates were immediately fixed with neutralized formaldehyde solution (4% v/v final concentration in seawater). After washing, organisms were separated according to their main taxonomical groups and preserved in ethanol 70°. All the animals were identified to the lowest possible taxonomical level under a stereomicroscope at 7-80X final magnification and counted. For organism identification, the taxonomical keys listed in Morri *et al.* (2004), were used. Abundance was expressed as number of individuals per m^2.

In order to investigate the functional structure of the community related to available food sources, two functional traits of paramount importance were considered: feeding habits and reproductive frequencies. Six different feeding habits were assigned to all individuals: surface deposit feeders (SDF), subsurface deposit feeders (SSDF), suspension feeders (SF), predators (P), omnivores (OMN) and grazers (G) using the following criteria: morphology of the feeding apparatus, feeding mode, nature and origin of the food. Three different types of reproductive frequencies based on their breeding were evaluated. Iteroparous (I), organisms breeding several times per lifetime; Semelparous (S), individuals that have only one brood during their life time and then the parent usually dies and Semi-continuous (C), reproduction occurs all year round or most part of the year.

Traits for each taxon were derived from literature sources and databases, namely Giangrande *et al.*, (1994);

Roth & Whilson (1998); MarLIN (2006); Jumars *et al.* (2015) and the Polytraits Team (2016).

Taxonomical resolution was kept at species level whenever possible but adjusted to genus or family when the information on traits was only available on a higher taxonomic level.

Statistical analyses

The diversity of the investigated macrofaunal community was evaluated using the following univariate community indices: abundance, species richness, diversity (H', Shannon & Weaver, 1949) and evenness (J', Pielou, 1966). The temporal variations of macrofaunal diversity were calculated by measuring turnover diversity (β_t) (Wilson & Shmida, 1984), which was calculated as follows:

$$\beta_t = \frac{[g(H) + l(H)]}{2\bar{\alpha}}$$

where g(H) is the number of species gained and l(H) the number of species lost, standardized by the average sample richness, and [$\bar{\alpha}$] is the average number of species found in the monthly samples.

Multivariate analysis of macrobenthic community structure was performed on the species abundance matrix applying a non-metric multidimensional scaling analysis (nMDS) ordination model. Monthly samplings were gathered in four seasonal groups based on bottom temperature: January, February and March as winter; April, May and June as spring; July, August and September as summer; October, November and December as autumn. Square root was used to transform the data matrix and Bray-Curtis similarity was applied. In addition, in order to highlight the variations of macrofaunal trophic habits and reproductive frequencies on a temporal scale, two bubble plots were applied to the nMDS ordination of seasonal abundance.

To detect which taxa were mainly responsible for changing species composition during this three-year study, SIMPER (SIMilarityPERcentage) analysis was employed and factor (years) was assigned. A log (X+1) transformation and a percentage dissimilarity cut-off of 70% were applied.

Similarity Profiles (SIMPROF) analysis was used to test whether taxa significant ($p < 0.05$) co-varied coherently, or rather to determine whether species were associated with each other in terms of numerical variation through the time-series. The taxa with an individual similarity contribute percentage >1 (SIMPER analysis) were used to perform SIMPROF analysis.

All univariate and multivariate analyses were performed using PRIMER 7 (PRIMER-E Ltd., Plymouth, UK) software (Clarke *et al.*, 2014).

The sum of monthly taxa abundances highlighted by SIMPROF was used to construct a Bray-Curtis dissimilarity matrix and an nMDS ordination. The environmen-

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tal (temperature and dissolved oxygen) and food sources (POC, TOC, BPC, MPBB and Meio) variables were overlaid as supplementary variables (vectors) onto ordination spaces to investigate their relations in this distribution. This vector fitting ordination was performed using the Vegan package in the R program (version 3.1.3).

In order to detect any changes at temporal scale, the monthly data of different food sources, feeding habits, reproductive frequencies and taxa abundances gathered by SIMPROF ($p < 0.05$) were split into two groups (2002-2003 and 2004-2005). The difference in the considered variables between these two periods was tested by Kruskal-Wallis ANOVA test.

The Spearman rank correlation test (r_s) was used to investigate relationships between food sources/feeding habits, reproductive frequencies and the taxa abundances gathered by SIMPROF ($p < 0.05$).

Kruskal-Wallis ANOVA and Spearman tests were conducted using STATISTICA 7 (StatSoft, Inc., USA) and only statistically significant data ($p < 0.05$, < 0.01) are presented.

Results

Environmental variables and food sources

The seawater temperature at the bottom varied from 6.5°C in February 2003 to 25.1°C in July 2003. Salinity ranged from 37.2 in June 2002 to 38.3 in February 2004. The lowest value of dissolved oxygen concentration was measured in August 2004 (59.1%) and the highest in April 2004 (120.2%). Over the study period, the lowest oxygen values were consistently observed in summer and autumn whereas they considerably increased from winter to spring due to vertical mixing and high primary production in the water column. Hypoxic conditions of the seabed were not recorded in this time frame (Table 1).

At the water column bottom layer, POC concentrations varied from 123.8 µg l⁻¹ in December 2004 to 358.5 µg l⁻¹ in June 2005. A seasonal pattern with a slight increase towards the end of the whole period was observed (Fig. 2a).

In the surface sediments, the lowest TOC contents were measured in November and September 2003 (7.4 ± 1.1 and 7.9 ± 0.2 mg g⁻¹, respectively), whereas TOC increased at the end of the study period (13.8 ± 0.2 mg g⁻¹ in July 2005). Indeed, significant differences in TOC content were observed between 2002-2003 *vs* 2004-2005 (H = 6.8; $p < 0.01$) (Fig. 2a).

BPC values were very low in 2002 and 2003 (minimum in June 2002 with 794.1 µg g⁻¹) while toward the end of the study period a major content was recorded (maximum in June 2005 with 2550.5 µg g⁻¹). Statistically significant differences in BPC content between 2002-2003 *vs* 2004-2005 (H = 10.6; $p < 0.01$) were observed (Fig. 2b). The PRT/CHO ratio values varied from 1.5 (June 2003)

Table 1. Temperature (°C), salinity and oxygen (%) of the water column at the sea bottom over the three-year study period.

	Temperature	Salinity	Oxygen
Jn'02	17.7	37.2	114.9
Jl'02	20.5	38.0	77.1
Se'02	23.0	38.2	81.6
Nv'02	15.9	37.7	94.9
Ja'03	10.2	38.1	97.8
Fe'03	6.5	38.1	94.4
Mr'03	8.3	38.1	101.2
Ap'03	9.9	37.9	98.1
My'03	11.3	38.0	111.0
Jn'03	15.3	38.0	120.1
Jl'03	25.1	38.2	114.8
Au'03	20.6	38.2	80.7
Se'03	20.8	38.2	85.0
Oc'03	17.0	38.1	85.4
Nv'03	13.9	38.2	91.9
De'03	11.4	38.1	90.8
Ja'04	8.6	38.3	90.6
Fe'04	7.5	38.3	92.7
Mr'04	8.0	37.9	95.5
Ap'04	10.5	38.0	101.6
My'04	14.2	37.6	104.9
Jn'04	16.9	37.3	95.5
Jl'04	21.0	37.6	77.4
Au'04	22.6	37.4	59.1
Se'04	22.0	37.3	94.8
Nv'04	15.0	37.1	95.0
De'04	14.1	37.9	94.1
Ja'05	7.3	38.2	98.8
Mr'05	6.7	38.3	104.7
Ap'05	10.2	37.9	96.8
My'05	12.9	37.8	99.0
Jn'05	18.6	37.9	94.9
Jl'05	19.9	38.0	93.6

to 6.6 (October 2003). Amplitude (indicated by the standard deviation) of this ratio was obtained by comparing the data of the first part of the study (2002-2003, mean PRT/CHO = 3.4 ± 1.5) with the more stable values from 2004 to the end of the sampling period (mean PRT/CHO = 3.3 ± 0.8).

MPBB varied between 5.7 µg C cm⁻³ in November 2002 and 39.6 µg C cm⁻³ in July 2005 and seasonal variations were noticed (Fig. 2b). Diatoms were the dominant

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microalgal group, representing up to 96.7% of total MPBB. At the end of the three-year study period, MPBB increased, mainly due to the development of the large diatom genus *Gyrosigma* spp. that peaked in July 2005 (10.3 µg C cm⁻³). The Meio-density ranged between 542 ± 83 ind.10 cm⁻² in January 2003 and 3345 ± 407 ind.10 cm⁻² in July 2003. Meio were dominated by Nematoda (72.0% of the total abundance), followed by Copepoda with their naupliar stages (18.0%) and Kinorhyncha (2.6 %) (Fig. 2b).

Like POC, MPBB and Meio showed a seasonal pattern over the study period, with a slight increase of MPBB and a decrease in Meio abundance towards the end of the three-year study period.

Macrofaunal community structure

The total abundance of benthic macrofauna at C1 did not show any seasonal pattern over the three-year study period. Abundance peaked in January 2002 (3283 ± 1753 ind. m⁻²), and high abundances (≥1700 ind. m⁻²) were also recorded in May 2003, March and August 2004, and in January 2005. The lowest values were measured in July 2003 (490 ± 533 ind. m⁻²) and in July 2002, March and June 2005 (<550 ind. m⁻²) (Fig. 3). Polychaetes were by far the dominant group, reaching 73.1% of total abundance over the whole study period, followed by molluscs (11.5%), crustaceans (9.8%), echinoderms (4.7%) and "others" (pooling the remaining groups which were rarely found: anthozoans, sipunculids and nemertines) (0.7%) of total abundance.

Up to 225 taxa were observed during the three-year study. The number of taxa ranged from a minimum of 38 (July 2002) to a maximum of 81 (January 2003 and August 2004) (Fig. 4a). No specific seasonal pattern was noticed during the study period and values remained fairly stable (average number of taxa 56.7 ± 11.1), though a large difference between the gained and lost taxa was observed between monthly samplings, indicating a high turnover ratio in the benthic community structure. During the three-year
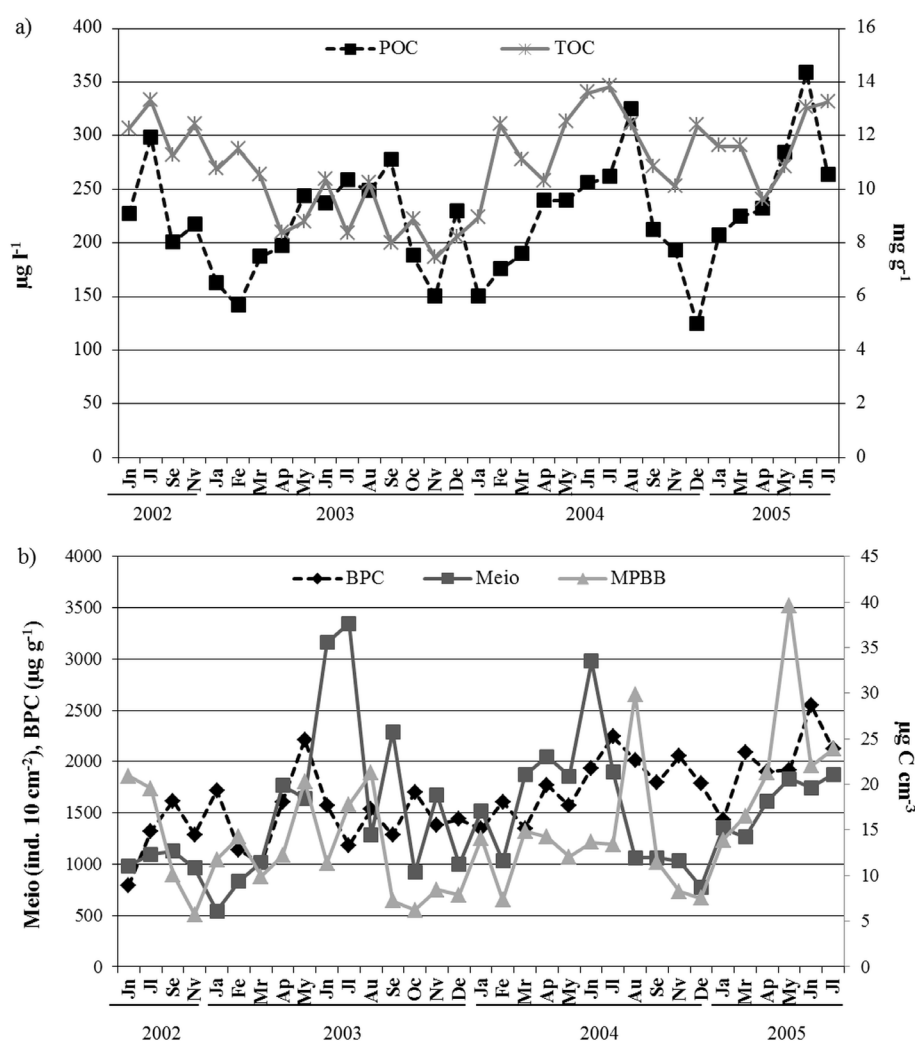

Fig. 2: Temporal variability of the food sources over the study period (2002-2005). a) POC= particulate organic carbon; TOC=total organic carbon. b) BPC = biopolymeric carbon; MPBB= microalgal biomass; Meio= meiofauna.
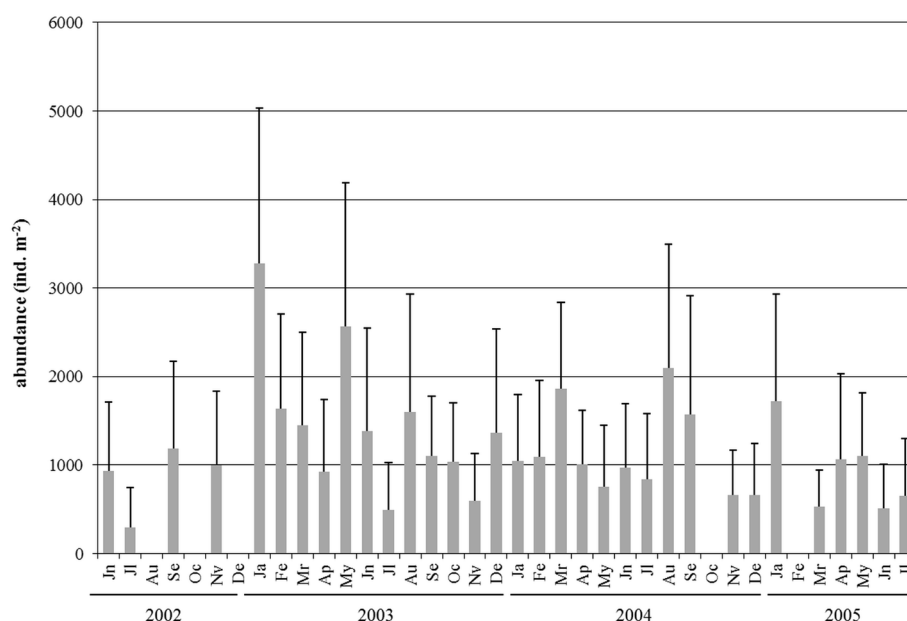
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Fig. 3: Macrofaunal abundance per m² (mean of three replicates and standard deviation) during the study period (2002-2005).

study period, turnover diversity (β_t) related to the variation in taxa composition, ranged from 0.3 (May 2003) to 0.6 (July 2002). Although the average values of turnover diversity between the first (2002-2003) and second (2004-2005) part of the study period remained stable (0.39 ± 0.10 and 0.38 ± 0.04, respectively), a major amplitude of β_t during the first years was observed (Fig. 4b). The values of Shannon's diversity and Pielou's evenness indices remained quite steady throughout the study period with an average of H' = 4.77 ± 0.25 and J' = 0.80 ± 0.05, respectively. Their lowest values were recorded in June 2002 (H' = 4.03 and J' = 0.71) whereas the highest ones were calculated in August 2003 (H' = 5.20) and July 2002 (J' = 0.93).

Functional characteristics of macrobenthos

The macrozoobenthic community was characterized by SDF (34.3%), followed by P (31.1%), SF (18.5%) and SSDF (13.1%). OMN and G were the least represented, 3% of the total community. All the trophic guilds, except for G, were recorded each month during the entire sampling period.

Community feeding habits did not show any clear seasonal variation during the three-year study (Fig. 5a). SDF peaked in January (1336 ± 517 ind. m⁻²) and May 2003 (976 ± 587 ind. m⁻²), in March (680 ± 318 ind. m⁻²) and August 2004 (636 ± 432 ind. m⁻²). A clear relationship between P and SDF was found over the study period, with

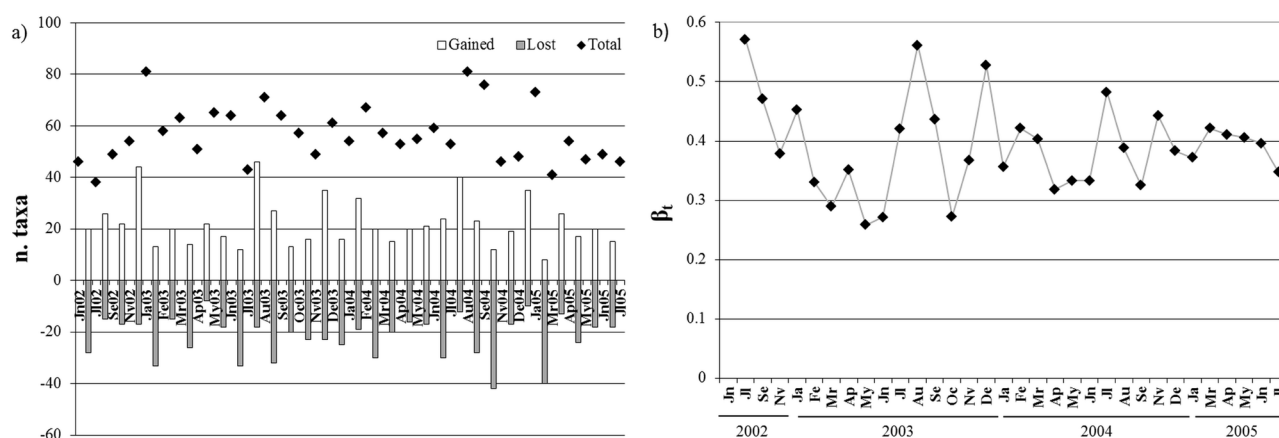**Fig. 4:** Number of taxa and turnover rates (taxa gained/lost at each sampling) (a) and β_t diversity (turnover diversity) (b) of soft sediment infauna over the study period (2002-2005)

a highly significant positive correlation between these two feeding habits ($r_s = 0.8$; $p < 0.01$).

In contrast, low values were recorded for SF and SSDF. SF varied from 83 ± 86 ind. m^{-2} in December 2004 to 510 ± 392 ind. m^{-2} in January 2003. The lowest value of SSDF was recorded in July 2002 (20 ± 34 ind. m^{-2}) and the highest in August 2004 (290 ± 234 ind. m^{-2}). Both feeding habit patterns remained unchanged over the study period.

As regards the reproductive strategies (traits) of the macrofaunal community, the I category was predominant (61.6% of total abundance) followed by S (36.5%), while the C frequencies displayed a negligible share (1.9%) (Fig. 5b). Similarly to the feeding habits, the reproductive traits showed unclear seasonal variation. However, similar dynamics of I and S abundance were observed during the study period as confirmed by a positive correlation ($r_s = 0.7$; $p < 0.01$). I abundances varied from 153 ± 301 ind. m^{-2} in July 2002 to 1296 ± 731 ind. m^{-2} in January 2003. S invertebrates peaked in January and May 2003 (1326 ± 470 and 960 ± 486 ind. m^{-2}, respectively). Furthermore, significant differences of S abundance between 2002-2003 *vs* 2004-2005 ($H = 10.56$; $p < 0.01$) were observed.

A highly significant relationship was observed between I and P ($r_s = 0.9$; $p < 0.01$) as well as between S and SDF ($r_s = 0.9$; $p < 0.01$). Considering the relationships among the food sources and reproductive frequencies, similar patterns were observed between S density and PRT/CHO ratio values on a temporal scale, as corroborated by a positive correlation ($r_s = 0.4$; $p < 0.05$) (Fig. 6).

The nMDS analysis based on macrozoobenthic species composition (Fig. 7a,b) highlighted a higher variability of the community among years than seasons. In this analysis, spring and autumn 2002, and winter 2003 were positioned on the left side of the plot at the maximum distance (Bray-Curtis maximum dissimilarity) from summer 2004 and summer 2005, indicating that during the three-year study period the community was subjected to significant temporal variations. These variations could not be attributed to feeding habits (bubble plot) that did not vary remarkably during the study period (Fig. 7a).

In contrast to feeding habit-traits, reproductive traits displayed a clear inter-annual pattern on a temporal scale (Fig. 7b). Most of the seasons of 2002 and 2003 were characterised by a higher abundance of S invertebrates
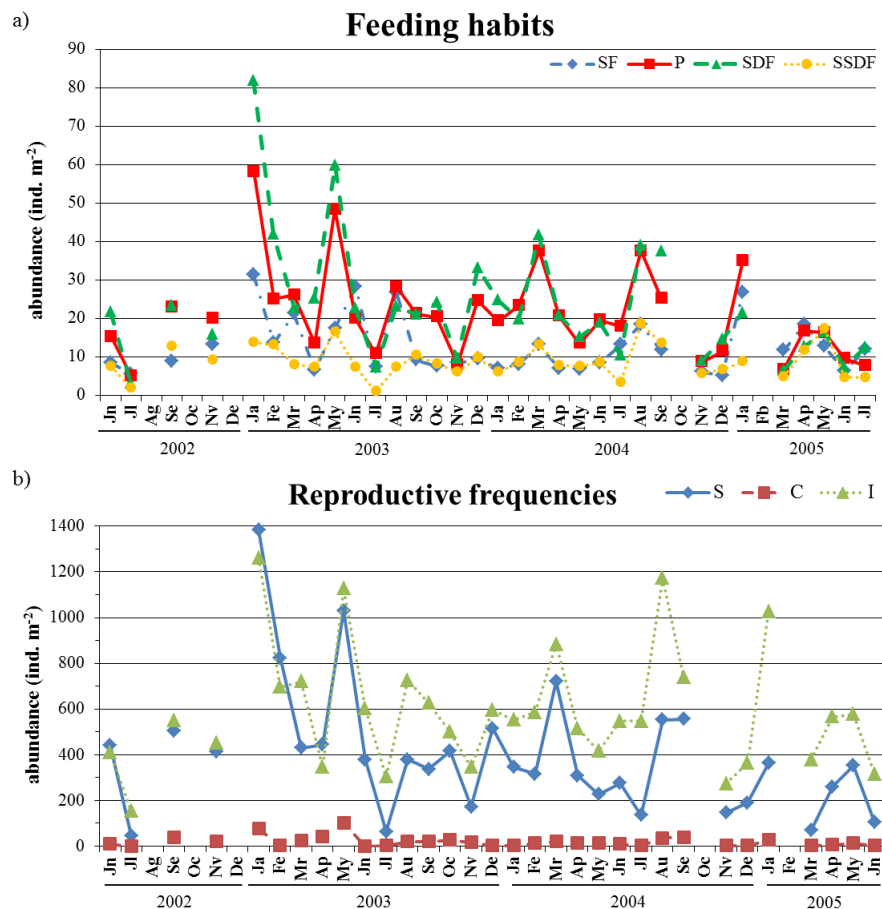

Fig. 5: Macrofaunal feeding habits (a): SDF=surface-deposit feeders; SSDF=subsurface-deposit feeders; SF=suspension feeders and P=predators (Omnivores and grazers are not reported) and (b) macrofaunal reproductive frequencies over the study period (2002-2005): C=semi-continuous; I=iteroparous; S=semelparous
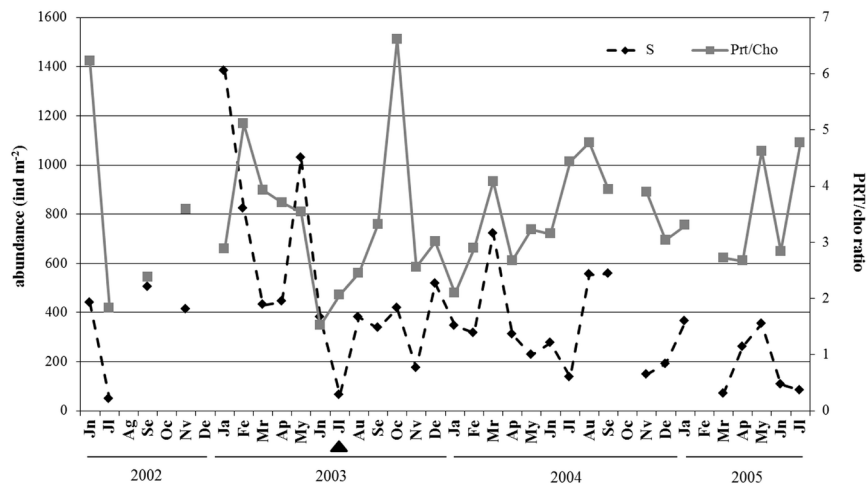
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Fig. 6: Co-variation of semelparous invertebrates and the protein/carbohydrates ratio (PRT/CHO ratio) over the three-year study (rs value = 0.36;p < 0.05). The black triangle indicates the heatwave event.
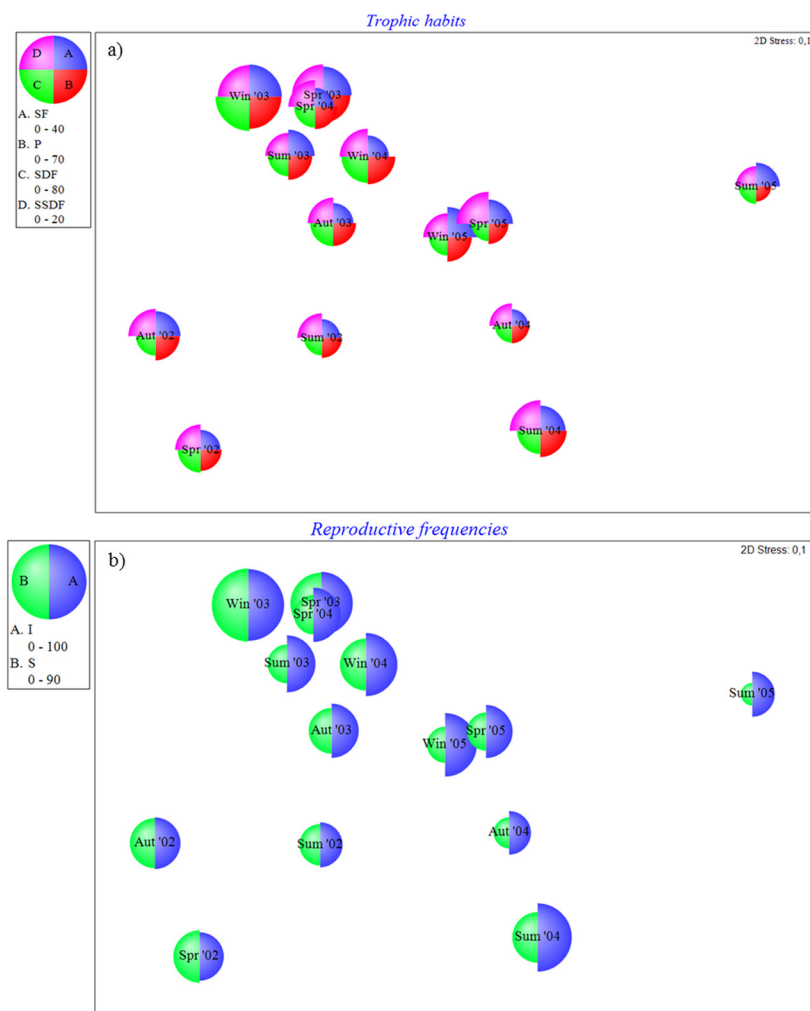

Fig. 7: Non-metric multidimensional scaling (nMDS) ordination plot of the biological matrix represented as segmented bubble plots.(a) Seasonal abundances of taxa with different feeding habits (omnivores and grazers are not reported) and (b) of reproductive frequencies (semi-continues are not reported). Spr=spring; Sum=summer; Aut= autumn; Win=winter.

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compared to I ones, which decreased during the seasons of 2004 and 2005.

Similarity Profiles analysis (SIMPROF) performed on the selected taxa with a percentage contribution >1 (highlighted by SIMPER analysis), illustrated four assemblages that significantly co-varied coherently during the three-year study. The abundances of the taxa gathered in the four groups represented, on average, 54.3 ± 8.3% of total macrofaunal density.

These four groups were characterized by the following taxa (Table 2 and Fig. 8):

1) the polychaetes *Prionospio cirrifera, Spirobranchus triqueter, Spiophanes kroyeri* and Syllidae and the crustaceans *Pisidia longimana* and *Phtisica marina* (Fig. 8a). Their abundance was higher in the first part of the study and then decreased towards the end of the period. *S. triqueter* was the most abundant taxon of this group, displaying higher values in August 2003 and January 2003 (226 ± 253 and 210 ± 200 ind. m^{-2}, respectively).

2) the polychaetes *Aricidea* sp., *Eunice vittata, Hilbigneris gracilis* and *Magelona* sp. (Fig. 8b). Considering the total density of *Aricidea* sp. over the study period (100%), they were divided as follows: 62.7% ('02-'03) to 31.1% (2004) and only 5.9% in 2005, remarkably decreasing towards the end of the study period. High values of *H. gracilis* were recorded over the period with an average of 180 ± 116 ind. m^{-2}. *E. vittata* showed decreasing values during the three-year study and significant differences in its abundances between '02-'03 *vs* '04-'05 (H = 7.9; *p* < 0.01).

3) the polychaetes *Labioleanira yhleni, Lumbrineris latreilli, Marphysa sanguinea, Melinna palmata* (Fig. 8c). High densities were observed from summer 2003 to spring 2004, particularly of the most abundant species *M. palmata* that reached its maximum in February 2004 (70 ± 45 ind. m^{-2}).

4) the polychaetes Maldanidae nd., *Pseudoleiocapitella fauveli* and *Scoletoma impatiens*, the crustacean *Am-*

Table 2. Minimum and maximum abundance (ind. m^{-2}) of the four groups of taxa highlighted by SIMPROF analysis and their feeding habits and reproductive frequencies.

Taxa	Range min-max (ind. m^{-2})	Feeding habit	Reproductive frequency
First group (G.1)			
Phtisica marina	0 - 63.3	Omnivorus	Semelparus
Pisidia longimana	0 - 56.6	Predator	Iteroparus
Prionospio cirrifera	0 - 90	Surface deposit feeder	Semi-continuous
Spiophanes kroyeri	0 - 126.3	Surface deposit feeder	Semi-continuous
Spirobranchus triqueter	0 - 226.6	Suspension feeder	Semelparus
Syllidae nd.	0 - 56.6	Omnivorus	n/d
Second group (G.2)			
Aricidea sp.	0 - 790.6	Surface deposit feeder	Semelparus
Eunice vittata	3.3 - 183.3	Predator	Iteroparus
Hilbigneris gracilis	6.6 - 443.3	Predator	Iteroparus
Magelona sp.	0 - 53.3	Surface deposit feeder	Semelparus
Third group (G.3)			
Labioleanira yhleni	0 - 36.6	Predator	Iteroparus
Lumbrineris latreilli	0 - 36.6	Subsurface deposit feeder	Iteroparus
Marphysa sanguinea	0 - 23.3	Surface deposit feeder	Iteroparus
Melinna palmata	3.3 - 70.3	Surface deposit feeder	Iteroparus
Fourth group (G.4)			
Ampelisca sp.	0 - 216.6	Suspension feeder	Iteroparus
Amphiura chiajei	3.3 - 60.6	Surface deposit feeder	Iteroparus
Antalis inaequicostata	0 - 26.6	Predator	Iteroparus
Maldanidae nd.	0 - 10	Subsurface deposit feeder	Iteroparus
Pseudoleiocapitella fauveli	0 - 30	Subsurface deposit feeder	Semelparus
Scoletoma impatiens	0 - 80	Surface deposit feeder	Iteroparus

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pelisca sp., the scaphopoda *Antalis inaequicostata* and the ophiuroid *Amphiura chiajei* (Fig. 8d). Their abundances increased towards the end of the study period. *Ampelisca* sp. was the most abundant taxon in this group reaching its maximum in January 2005 (216 ± 25 ind. m^{-2}). *S. impatiens* and *A. chiajei* were abundant with highest density in August 2004 (80 ± 43 and 60 ± 47 ind. m^{-2}, respectively). Statistically significant differences between '02-'03 *vs* '04-'05 were recorded for *Ampelisca* sp and *S. impatiens* (H = 4.7 and H = 6.6; *p* < 0.05, respectively) and for *A. chiajei* (H = 10.0; *p* < 0.01). This latter taxon was also related to an increase of BPC and MPBB (r$_s$ = 0.6; *p* < 0.01 and 0.3; *p* < 0.05, respectively). Other positive correlations were also obtained between different food sources and taxa gathered in this assemblage. *A. inaequicostata* was correlated with POC, BPC and MPBB (r$_s$ = 0.4, 0.5; *p* < 0.01 and 0.4; *p* < 0.05, respectively). Maldanidae nd. was related to TOC and BPC (r$_s$ = 0.4 and 0.4; *p* < 0.05).

The vector fitting *n*MDS analysis based on the monthly abundances of the four groups of taxa and the superimposed environmental parameters (temperature, oxygen concentration and food sources) showed a variation in taxa composition on a temporal scale. Community composition differed to a higher extent among years than seasons. In the ordination plot, a temporal pattern of monthly taxa was observed. Specifically, a variation in species distribution of the gathered taxa from the lower left corner of the graph (2002 and 2003, except for July

2002) (G.1 and G.2. in Fig. 9) to the upper right one (2004 and 2005) (G.3 and G.4 in Fig. 9) was displayed (dotted line). The environmental parameters - TOC, POC, BPC and MPBB - were plotted spatially close to G4 (towards the upper part of the ordination); conversely, Meio and above all temperature, were located in the opposite direction, relatively close to G.2 and G.3 (towards the lower part of the plot).

Discussion

Our results revealed higher variability of the macrozoobenthic community structure among years rather than seasons. This is in disagreement with the general pattern for the Mediterranean Sea, where most of the benthic species exhibit a seasonal pattern, with reproduction in spring or autumn and growth from autumn to spring (Coma *et al.*, 2000). The primary forcing of changes in benthic communities often occurs during a distinct period of seasonal cycles, e.g. caused by food supply due to sedimentation of the spring phytoplankton bloom (Cibic *et al.* 2007b) or by oxygen deficiency due to high temperatures in late summer (Reiss & Kröncke, 2005). Although our results do not follow this general pattern dictated by seasonality, they are in accordance with those reported by Clarke & Frid (2001), Warwick *et al.* (2002) and Rousi *et al.* (2013) who also observed major yearly differences
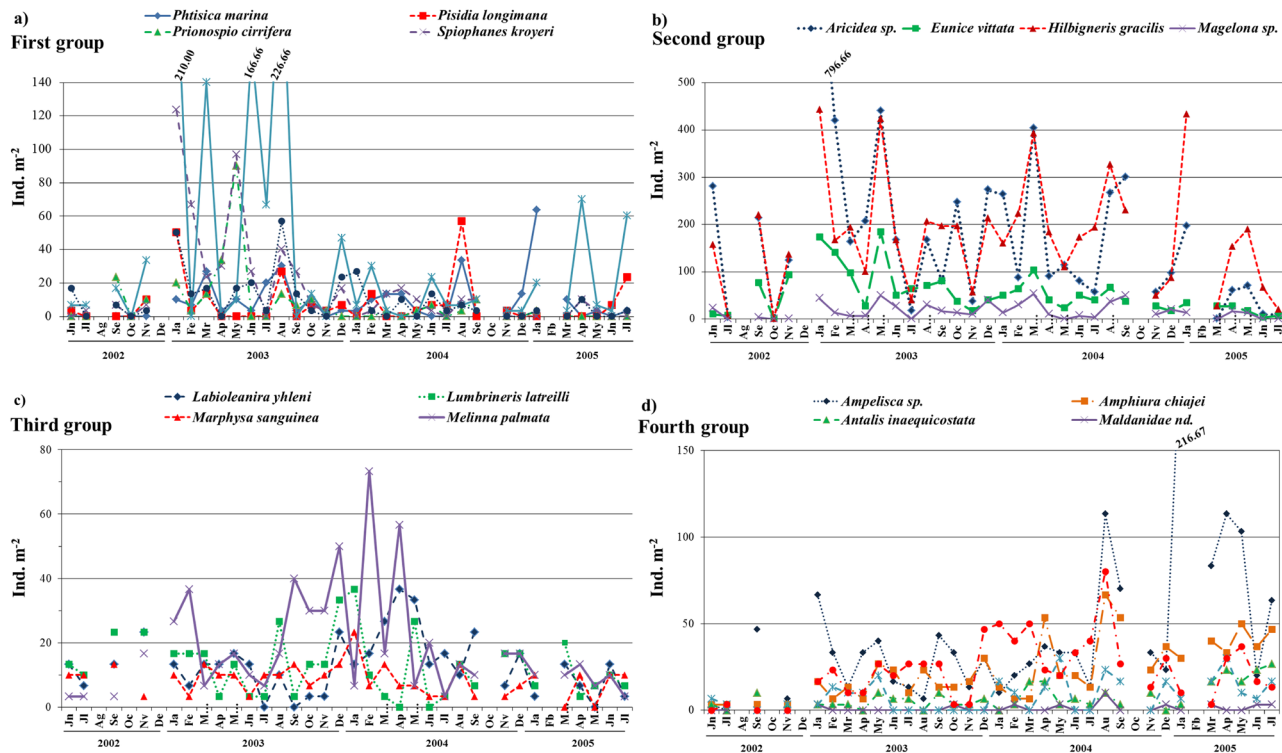

Fig. 8: Temporal variation of taxa gathered by SIMPROF (p<0.05) over the study period (2002-2005).
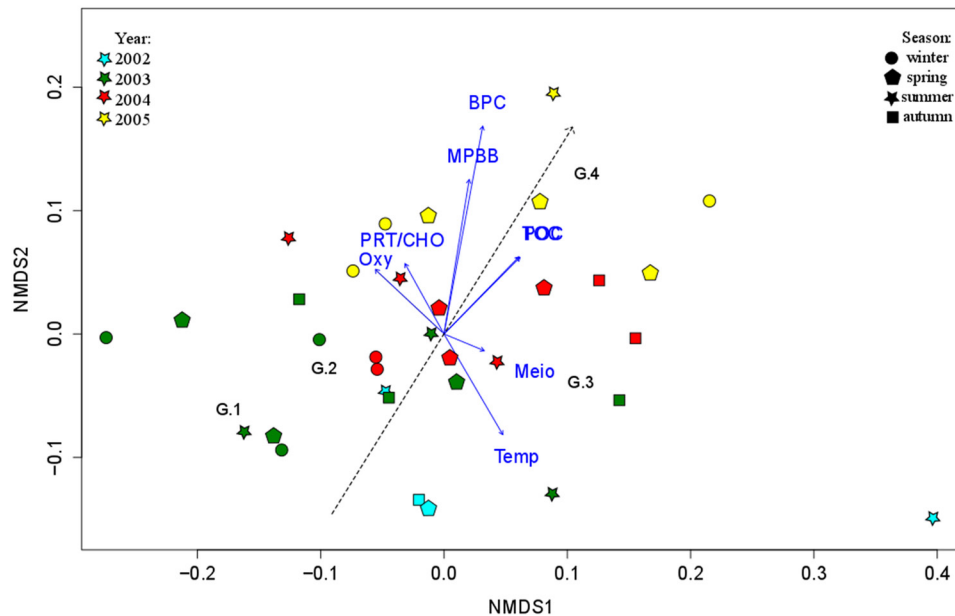
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Fig. 9: nMDS ordination plot based on the taxa abundance gathered by SIMPROF. Temperature, dissolved oxygen and food sources (blue arrows) were plotted using vector fitting with ordination scores (stress value 0.13). Temp= temperature; Oxy= dissolved oxygen; POC= particulate organic carbon; TOC = total organic carbon; BPC = biopolymeric carbon; PRT/CHO=protein-carbohydrate ratio; MPBB= microalgal biomass; Meio= meiofauna. Years are indicated with different colours and seasons with different shapes. Temporal variation (from 2002 to 2005 indicated as a dotted line) in species distribution of the gathered taxa. TOC and POC are overlaid. For groups description see Table 2.

in macrofaunal structure rather than seasonal ones. According to the findings of these authors, macrofaunal development was strictly linked to particular environmental variations, such as changes in grain size, sedimentation rate and high temperature.

The taxonomic composition of the macrofaunal community during the study period revealed a typical community of sandy-mud and detrital sediments, as previously reported for the Gulf of Trieste (Mavrič *et al.*, 2010; Faresi *et al.*, 2012), for the northern Adriatic Sea (Simonini *et al.*, 2004; Occhipinti-Ambrogi *et al.*, 2005; Franzo *et al.*, 2015), and worldwide (Warwick *et al.*, 2002; Rousi *et al.*, 2013; Somerfield *et al.*, 2014).

Focusing on the food sources for the macrofaunal community, a clear seasonal pattern was observed for POC, MPBB and Meio. POC slightly increased towards the end of the study period probably after a phytoplankton bloom that occurred in summer 2004 and spring 2005 (Cabrini *et al.*, 2012). In contrast, TOC and BPC contents exhibited high variability between the two periods ('02-'03 *vs* '04-'05) as corroborated by the Kruskal-Wallis analysis (H = 10.6; *p* < 0.01). TOC generally exhibits a more conservative nature. This suggests that changes in the quantity of BPC might respond to changes in the trophic status more promptly than TOC (Pusceddu *et al.*, 2009). In fact, in our study, the macrofaunal community was subjected to high organic matter availability in 2002 that gradually decreased towards autumn 2003. Afterwards, TOC values

increased again reaching their maxima in June 2005. In contrast, this was not observed for BPC that did not show a remarkable decrease in autumn 2003 but higher values were displayed towards the end of the three-year study period, corresponding to major MPBB. The increase of MPBB in the sediment surface layer might have modified the quality of organic matter, rendering it more palatable, as already highlighted by Hardison *et al.* (2013). PRT/CHO <1 suggests the presence of aged organic matter (Dell'Anno *et al.*, 2002). In our study, the ratio ranged from 1.5 (June 2003) to 6.6 (October 2003) indicating the availability for benthic organisms of freshly produced organic matter over the entire period, even though wide fluctuations of the ratio were observed especially in the first part of the study (2002-2003, see Fig. 6).

Feeding habits and reproductive frequencies in relation to food sources

During the entire study period, biological traits related to feeding habits were not influenced by the naturally occurring physical fluctuations at the sampling site (St. C1), showing unclear variability over the study period (see Fig. 5a and 7a). SDF remained the most common trophic trait category, probably due to the even and stable grain size-distribution (Cibic *et al.*, 2012 and Franzo *et al.*, 2016) This is in accordance with Simonini *et al.* (2004); Occhipinti-Ambrogi *et al.* (2005) and Faresi *et al.* (2012),

who found deposit feeding invertebrates to be numerically dominant in sandy-mud or muddy sediments. Much of the detrital food for these invertebrates is associated with a high proportion of particles within the silt-clay range. The high surface-area-to volume ratios of small particles provide a large expanse for the attachment and growth of microbial populations that produce mucopolysaccharide exudates, which are very palatable for these invertebrates (Donald & Larry, 1982 and reference therein).

Some SDF displayed opportunistic behaviour. Favourable environmental conditions, following an increase of food supply, could rapidly stimulate the growth, reproduction rate and survivorship of individuals. After consumption of the peaks in food and/or being consumed by P, SDF abundance could decrease considerably, suggesting wide temporal fluctuations (Rossi, 2003 and references therein).

The SDF are not bulk ingestors of surface sediments, but rather they are able to modify their behaviour and choose to feed on fresh organic matter at very small spatial scale (Cruz-Rivera & Hay, 2000a). Experimental studies (Bolam & Fernandes, 2002; Rossi, 2003; Levinton & Kelaher, 2004) have highlighted that the presence of food patches in the sediments could increase the frequency at which they move and stay in those patches because of a more suitable micro-habitat, with a consequent increase in individual abundances.

In this macrofaunal community, P as a feeding category followed the pattern of SDF (r_s=0.6; p<0.01). P probably prayed on the numerically dominant species, as suggested by Quijón & Snelgrove (2005). In fact, SDF aggregated in high abundance soon after the establishment of patches, and thus the subsequent arrival and feeding by mobile predators could be a real possibility.

In the first part of the study (2002 and 2003), the majority of SDF individuals belonged to S species, as corroborated by the significant correlation between these two traits. These species are considered *r*-strategists with an opportunistic response or, rather, are short-lived invertebrates with fast growth, early maturity and high fecundity that increase in abundance when a fresh food supply is available (Gray & Elliott, 2009). The S polychaetes such as *Aricidea* sp., *P. cirrifera*, *S. kroyeri* and *S. triqueter* were numerically dominant in the first part of the study period. These taxa displayed unpredictable changes in abundance in response to high and irregular input of organic matter. In fact, high individual density and irregular peaks were observed in correspondence with wide variations of the PRT/CHO ratio in the first part of the study period that might have favoured the growth of opportunistic/*r*-strategist species (also corroborated by the S and PRT/CHO positive correlation). Our findings are in accordance with other studies from coastal areas, which have reported wide variations of food supply due to the intrinsic features of these sublittoral environments (i.e. highly variable hy-drodynamics, runoff, sedimentation and turbidity) (Ellis *et al.*, 2000 and reference therein).

Over the three-year study period, a higher density of P was observed compared to the other feeding habits; the majority of P were also I organisms (r_s = 0.9; p < 0.01), indicating that this trophic guild presented different reproductive features compared to the majority of SDF invertebrates. For instance, I is a reproductive trait typical of *K*-strategists; they breed several times during their lifetime, are characterised by delayed reproduction, slow growth and longer life span with a less pronounced numerical fluctuation than S invertebrates (Giangrande, 1997). Towards the end of the 2004-2005 period, the monthly abundances of P were generally higher than those of deposit and suspension feeders. This may indicate that macrofaunal P preyed on Meio invertebrates. The potential top-down control on meiobenthic invertebrates by macrofaunal P has been reported often (Van Colen *et al.*, 2015). In fact, as found by Jumars *et al.* (2015), many polychaetes observed at our study site belong to the families Lumbrineridae and Eunicidae (mainly *Lumbrineris gracilis* and *Eunice vittata,* respectively). They have paired mandibles and complex sets of maxillae in a strongly muscular and eversible pharynx and are able crawlers and burrowers in muddy sediments and, therefore, they could be potential Meio predators.

As highlighted by the vector fitting nMDS analysis, the last part of the study period was characterized by a community shift likely related to the increased food supply, particularly POC, BPC and MPBB. The species observed during this time frame were principally SDF and I. While the feeding strategies did not remarkably change during the three-year study, the quantity and quality of food supply did. We infer that the high abundances of *A. Chiajei* and *A. Inequicostata* observed in last part of the study were a result of the high availability of BPC (r_s = 0.7, 0.5; p < 0.01). Sköld & Gunnarsson (1996) and Nilsson (1999) previously observed an increase of *A. chiajei* in response to food pulses. Their findings showed that brittle stars are capable of increasing their growth and gonad development in response to short-term fresh organic matter-enrichment and even more with a diet based on diatoms. Indeed, in our study, A. *chiajei* was correlated with MPBB (r_s = 0.4; p < 0.05). MPBB is the preferred food source of many soft-sediment benthic invertebrates. In marine systems, a high amount of energy (C flow) is directly transferred from primary producers to consumers (Cruz-Rivera & Hay, 2000b). The high amount of lipids (e.g. triglycerides and long fatty acid chains) contained in microalgal cells makes them very palatable to deposit feeder invertebrates (Goedkoop *et al.*, 2011). Similarly, the Scaphopoda *A. inequicostata* was correlated with MPBB and POC (r_s = 0.4; p < 0.05; r_s = 0.4; p < 0.01, respectively). A major fraction of this POC at St. C1 is probably ascribable to phytoplankton cells. The occurrence of a high abundance of SDF has been related to the sinking

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of phytodetritus (Quijón *et al.*, 2008 and reference therein). According to the review of Reynolds *et al.* (2002) on the Scaphopoda class, *A. inequicostata* has often been classified as a predator, but it has also been reported as a deposit or suspension feeder, feeding on foraminifers and other microorganisms (diatoms) using its tentacles.

Macrofaunal community development on a temporal scale

Persistent and stable benthic communities have generally been related to environments that are free of disturbances with relatively stable physical parameters (Buchanan *et al.*, 1986). These communities are not characterised by remarkable variability in their structure (biodiversity and functional characteristics of species) and, in addition, the absolute abundance of each species remains constant over time (Turner *et al.*, 1995). On the contrary, unstable communities usually display high biodiversity variability, changes in species composition and especially wide fluctuations in species richness and J' values (Worm & Duffy, 2003). In this three-year study, the macrofaunal community showed quite high and fairly stable diversity indices values (species richness, H' and J'), although several changes in community composition were observed during this period that were revealed by the high amplitude of turnover biodiversity. The turnover values obtained towards the end of the study were high compared to those reported in the literature (Wilson & Shmida, 1984; Quillien *et al.*, 2015). In detail, turnover biodiversity values ($\beta_t = 0.39 \pm 0.10$) displayed a wide range in amplitude in the first period (2002 and 2003) compared to the second one ($\beta_t = 0.38 \pm 0.04$) (2004 and 2005), indicating high variability in species turnover with slight stabilization towards the end of the study. Overall, high biodiversity and monthly turnover diversity suggest an intermediate level of stability. Indeed, although changes in community structure were observed by vector fitting nMDS analysis, some species were present throughout the study period. According to Huston (1994) and Sommer & Worm (2002), the highest biodiversity often occurs at intermediate levels of disturbance intensity or frequency, and, by inference, at an intermediate level of community stability. In addition, at this level of stability, the macrofauna displayed minor variability in species composition but larger population fluctuations that primarily involved relatively short-lived invertebrates (with year-to-year variability) (Gray & Elliott, 2009 and references therein). We believe that the variations in dominant species composition and reproductive frequencies were mostly a consequence of the heatwave observed in summer 2003, rather than ascribable to the concomitant high values of BPC and MPBB. In fact, irregular high sea bottom temperatures were observed in summer 2003 (25°C in July), more than 3°C above the average summer values recorded over a 12-year study in the Gulf of Trieste (Malačič *et al.*, 2006). This was the warmest summer recorded in the Mediterranean Sea in

the last few decades (Schär *et al.*, 2004). This physical stress might have led to long-term changes in macrofaunal individual abundance, biodiversity and taxa composition and their functional traits.

As reported by Crisci *et al.* (2011), this heatwave caused irregular seawater warming, reaching temperatures between 1 and 3 °C above the climatic values in several areas of the Mediterranean Sea and consequent mass mortality events of benthic macroinvertebrate species occurred (Garrabou *et al.*, 2009). In spite of these high temperatures in summer 2003, dissolved oxygen concentrations at St. C1 were not under-saturated, and therefore no mass mortality was observed that might have been expected following this heatwave. Macrofaunal community biodiversity did not seem to be affected by this drastic pulse of environmental change. H' values remained within in the same range of the study period (H' = 4.9 and 5.0, in July and August 2003, respectively). Community resistance to this physical stressor could be attributed to its adaptation to the highly variable local environmental conditions. In the Gulf of Trieste, sea bottom temperatures display wide annual fluctuations (from 6°C to >20°C) that have likely selected macrofaunal communities with adaptation mechanisms in response to temperature stress. Communities of unstable environments are more preadapted to fluctuations (Munari, 2011). The same finding was obtained both from field studies (Fitt *et al.*, 2001) and experimental ones (Torrents *et al.*, 2008) carried out on benthic invertebrates. The authors concluded that thermotolerance can vary among populations of the same species and the upper thermal limits are correlated with their different temperature environment and previous stress history. In fact, in 2003, the highest (25.1 °C in July) and the lowest (6.5 °C in February) sea bottom temperatures were measured at St. C1 over the three-year study period.

However, the high temperatures in summer 2003 might have strongly affected macrozoobenthic reproductive frequencies. The abundance of I invertebrates, although presenting numerous density peaks, remained relatively stable during the entire study period (see Fig. 5b and 7b). On the other hand, S organisms were very abundant in the first part of this study (2002-2003), reaching higher abundances than I organisms (i.e. January, February and April 2003). After the summer of 2003, a significant decline was observed and even low density was noticed towards the end of the study period, as shown by the Kruskal-Wallis analysis (H= 10.6; *p* < 0.01).

Overall, low abundances of S organisms were recorded each summer, although the heatwave of 2003 might have modified their fitness (i.e. the ability of a population to maintain or increase its abundance in succeeding generations). In fact, after these extreme events, they did not reach comparable densities to those observed in the previous periods (2002 and winter-spring of 2003) (see Fig. 7b).

Even I organisms were negatively influenced by the high temperatures recorded in summer 2003. Their density slightly decreased in July 2003 but then they recovered towards the end of study. Since the heatwave lasted a short period of time, it is likely that the high temperatures affected S species (*r*-strategist) primarily, which were less stress-resistant. In contrast, the long-lived iteroparous organism (*K*-strategist) are better buffered from extreme environmental events; their population size does not vary as much as that of smaller, shorter-lived organisms. Furthermore, their competitive relationships are presumably more predictable and constant (Pianka, 1970; Ranta *et al.*, 2002; Gray & Elliott, 2009).

We infer that I invertebrates at St. C1 were able to resist stress caused by temperature due to the ecological features of *K*-strategist species that allow them to prevail over *r*-strategists in inter-species competition even when the heatwave was over.

Conclusion

During the three-year study, the macrofaunal community at St. C1 displayed higher variability among years than seasons. A remarkable temporal variation in taxa composition was observed due to a shift in their reproductive frequencies: from the dominance of S invertebrates to I ones. In spite an increasing food supply over time, the variations in macrofaunal structure were likely linked to the heatwave occurred in 2003. S organisms were less resistant to high temperatures compared to I ones. The latter were able to resist temperature stress, allowing them to prevail over S species in inter-species competition even when the heatwave was over.

Overall, the community displayed an intermediate level of stability from high diversity and unvarying feeding habits to high turnover diversity and variations in reproductive frequencies. The capability of the community to maintain a similar structure (abundance, biodiversity and feeding strategies), despite remarkable physical disturbance events, further testifies the resistance exhibited by macrofaunal invertebrates. The functional traits approach applied in this study allowed to identify the role of environmental factors and food supply on the temporal development of the macrofaunal community.

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