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► **To cite this version:**

Luigi Musco, Barbara Mikac, Mariella Tataranni, Adriana Giangrande, Antonio Terlizzi. The use of coarser taxonomy in the detection of long-term changes in polychaete assemblages. *Marine Environmental Research*, 2011, 71 (2), pp.131. 10.1016/j.marenvres.2010.12.004 . hal-00664017

HAL Id: hal-00664017

<https://hal.science/hal-00664017>

Submitted on 28 Jan 2012

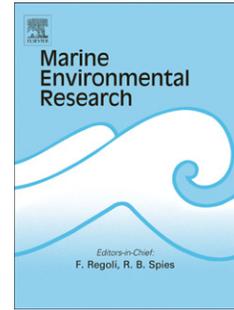
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Accepted Manuscript

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PII: S0141-1136(10)00179-0

DOI: [10.1016/j.marenvres.2010.12.004](https://doi.org/10.1016/j.marenvres.2010.12.004)

Reference: MERE 3492

To appear in: *Marine Environmental Research*

Received Date: 2 November 2010

Revised Date: 6 December 2010

Accepted Date: 8 December 2010

Please cite this article as: Musco, L., Mikac, B., Tataranni, M., Giangrande, A., Terlizzi, A. The use of coarser taxonomy in the detection of long-term changes in polychaete assemblages, *Marine Environmental Research* (2010), doi: [10.1016/j.marenvres.2010.12.004](https://doi.org/10.1016/j.marenvres.2010.12.004)

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The use of coarser taxonomy in the detection of long-term changes in polychaete assemblages

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ABSTRACT

Taxonomic Sufficiency (TS) has been proposed as a short-cut method to quantify changes of biological assemblages in environmental monitoring. However, issues about the efficacy of taxonomic surrogates in depicting long-term temporal patterns of marine assemblages are still scant. Here we report on the adoption of TS combined with data transformations to describe patterns of North Adriatic polychaete assemblages through 20 years. Univariate and multivariate analyses revealed large spatial-temporal variation characterizing the assemblages. The efficiency to discriminate between the two research periods (1990-1994 vs. 2004-2008) was reduced when data were analyzed at family and order level leading to misinterpreting the sources of assemblage variation. Further information was lost with data transforms. Families may represent appropriate assemblages' descriptors in long-term monitoring, but using TS coupled with data transformations could lead to hazardous loss of information. We suggest that periodical analysis at fine taxonomic level should be routinely alternated to long-term monitoring based on TS in order to check its effectiveness.

Keywords: Taxonomic sufficiency, biomonitoring, Polychaetes, anoxia, temporal variability, taxonomy, Adriatic Sea

1. INTRODUCTION

1 Assessing long-term changes in natural systems (i.e. recovery after mass mortality, effects of
2 restoration or protection, climate change etc.) is one of the most intriguing challenges for
3 quantitative ecology.

4 In marine environments, measuring patterns of variation in benthic assemblages can provide the
5 most useful information for interpreting the ecological consequences of disturbances and furnish the
6 basis for understanding environmental changes (Underwood, 1996; Underwood and Peterson,
7 1988). In this context, the benthic macrofauna is particularly suitable for monitoring environmental
8 long-term changes at the ecosystem level (Kroncke, 1995).

9 Describing assemblages at the highest levels of taxonomic resolution (species) is logistically
10 difficult due to high cost in processing samples and, above all, lack of taxonomic expertise. The
11 development of fast and cost-effective procedures in impact assessment and monitoring studies has
12 become a pressing issue for marine ecologists (Bowen and Depledge, 2006; Uglund et al., 2008). In
13 such context, Taxonomic Sufficiency (TS) (Ellis, 1985), which implies “identifying organisms only
14 to a level of taxonomic resolution sufficient to satisfy the objective of a study” (Bertrand et al.,
15 2006), has been proposed as the ideal compromise procedure in environmental monitoring. TS is
16 supported by evidences that impacts could be detected using coarser taxonomic resolution since
17 abundance/diversity of species are usually related to abundance/diversity of the same organisms
18 identified to supra-specific taxonomic levels (Genus, Family, Order etc.) (e.g. Balmford et al.,
19 1996). It has also been suggested that higher taxa may reflect the effect of anthropogenic
20 disturbance even better than species, being the latter more sensitive to the confounding influence of
21 natural environmental variations (Warwick, 1988; Vanderklift et al., 1996). In general, no
22 significant losses of information, as well as time and costs savings, are the argumentations
23 supporting the TS method in environmental impact assessment (Dauvin et al., 2003, 2010; Herman
24 and Heip, 1988; Munari et al., 2010).

25 Currently, lacking a general theory on TS, reasons at the base of the effectiveness of TS are still far
26 to be clarified (Dethier and Schoch, 2006). Understanding at which extent functional redundancy
27 overlap taxonomic relatedness of species, would help to provide a general framework on the
28 application of TS in marine systems (Bevilacqua et al., 2009). The need to broaden the array of
29 study cases on the application of TS has been repeatedly stressed (e.g., Bates et al., 2007; Olsgard
30 and Somerfield, 2000; Quijón and Snelgrove, 2006; Terlizzi et al., 2003), because possible biases of
31 TS are to be further investigated. The significance of the Linnaean ranks is being criticized so far as
32 the treatment of same taxonomic ranks as equivalent units is suspected to allow to spurious
33 comparisons (see Bertrand et al., 2006). The extent to which TS affects the results depends on the
34 distribution of species amongst higher taxa in the original samples, that, in turn depends on habitat

1 type and bio-geographic background (Musco et al., 2009; Terlizzi et al., 2009). Further, the relation
2 among TS, and data transformation is far to be fully clarified. Several studies showed that
3 transforming data might influence the results of analyses as well as taxonomic aggregation,
4 suggesting that the use of TS coupled with strong transformations of data could lead to severe loss
5 of information (Lasiak, 2003; Olsgard et al., 1998; Wlodarska-Kuwalczyk and Kedra, 2007).

6 As far as long-term monitoring studies are concerned, the use of coarser taxonomic level, being
7 time-efficient, could improve monitoring programs allowing the extension to additional sampling
8 dates (Thompson et al., 2003; Tataranni et al., 2009). Some loss of information on community
9 structure is considered acceptable for extensive monitoring purposes, and the detection of
10 biodiversity changes should be admissible as well (Bertasi et al., 2009). However, studying the
11 long-term recovery pattern of polychaete assemblages of Botany Bay (NSW, Australia), Fraser et
12 al. (2006) found that the importance of differences in assemblage structure, as well as patterns of
13 succession, could not have been examined in detail using TS. The same Authors suggest that
14 analysis of data at various taxonomic levels, after identification of organisms to species, should be
15 encouraged in long-term impact-assessment studies. This issue, however, is made difficult by the
16 lack of long-term monitoring programmes based on the description of variables at species level. The
17 present study is an attempt in this direction.

18 Polychaetes are widely distributed, abundant and diverse in terms of species richness and ecological
19 requirements and have been successfully used as indicator taxon (Giangrande et al., 2004, 2005;
20 Musco and Giangrande, 2005; Frascchetti et al., 2006; Musco et al., 2009) also in long-term
21 monitoring studies (Fraser et al., 2006; Schirosi et al., 2010). Here, we compared the effects of
22 taxonomic aggregation and data transformation on the analysis of multivariate patterns of variations
23 related to the decadal changes of the polychaete assemblages, following mass mortality caused by
24 the oxygen depletion in the Northern Adriatic Sea in 1989.

25

26 **2. Materials and Methods**

27

28 **2.1. Research area**

29 The Northern Adriatic Sea (hereafter NA) is a semi-enclosed shallow basin exposed to severe
30 human impacts such as strong urban development, high nutrients load, commercial fisheries and
31 different kinds of pollution (Degobbis et al., 2000). Sometimes, when mucilage events coincide
32 with specific hydrographical conditions, anoxia may affect the sea bottom. Such an event happened
33 in the autumn 1989 and caused benthic mass mortality over an area of about 1.200 km².

1 The study was carried out on three offshore monitoring stations of the Centre for Marine Research
2 (Ruđer Bošković Institute, Rovinj) located within the affected area. Station SJ 005 (hereafter 005)
3 (45°18.4' N; 13°18.0' E; 31 m depth) and station SJ 007 (007) (45°17.0' N; 13°16.0'E; 31 m depth)
4 are situated on the profile Poreč (Croatia) - Venice-Lido (Italy), 17 and 13 NM off from the coast of
5 Istrian peninsula (Croatia), respectively. Station SJ 107 (hereafter 107) (45°02.8 N; 13°19.0' E; 37
6 m depth) is situated on the profile Rovinj (Croatia) - river Po delta, 13 NM off the Istrian coast (Fig.
7 1). Granulometric analyses showed high similarity in sedimental composition among the three
8 stations. Sediment is weakly sorted silty sand composed mainly by sand (ranging 66.3 - 70.6 %),
9 followed by silt and clay fraction (27.8 - 32.1 %) and gravel (1.4 - 1.6 %).

10

11 **2.2. Field and laboratory work**

12 Starting one year after the anoxia event, samples were taken once a year, in two phases during
13 1990-1994 and 2004-2008, in the period from late October to the beginning of January .

14 At each station 4-5 replicates were collected with 0.1 m² Van-Veen grab, sieved through 2 mm
15 mesh in the first research period (1990-1994) and 1 and 2 mm mesh in the second one (2004-2008),
16 and fixed in 4% buffered formaldehyde-seawater solution. As a whole, 113 samples were collected.

17 The 1 mm mesh size in the second period was adopted following the up-to-date recommendation
18 for the macrobenthic fauna monitoring studies provided by Castelli et al. (2003). However, for the
19 present study, in order to allow long-term comparisons, only 2 mm mesh size samples were used. In
20 the laboratory the material was rinsed and macrobenthic organisms sorted and conserved in 70%
21 ethanol. Polychaetes were determined to the species level using the stereomicroscope and light
22 microscope. Nomenclature followed Castelli et al. (2008).

23

24 **2.3. Data Analysis**

25 Three separate analyses of variances (ANOVAs) were performed to test the null hypotheses of no
26 differences among polychaete assemblages in number of individuals, species richness and Simpson
27 diversity index. The experimental design included three factors: Period (Pe, a fixed factor with 2
28 levels), Time (T, random, with 9 levels and nested in Pe) and Station (S, random, with 3 levels and
29 crossed to both Pe and T).

30 The same sampling design was used, in the multivariate context, to perform a distance-based
31 permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), which used 999
32 random permutations of appropriate units to test for differences in the polychaetes assemblages'
33 structure among periods across the three stations. The analysis was based on untransformed data at
34 species level. In order to quantify the variability associated with each examined scale, mean squares

1 calculated by PERMANOVA were equated to the expected mean squares, like in the univariate case
2 (Benedetti Cecchi, 2001; Searle et al., 1992). For graphical comparisons, the variability at each
3 scale was expressed as a proportion of the total variation (Terlizzi et al., 2007). The same analyses
4 were then repeated for the dataset lumped at genus, family and order taxonomic level.
5 PERMANOVAs were also carried out for calculating estimates of variance components using 2nd
6 root, 4th root and presence/absence transformed data for all the taxonomic levels investigated.
7 Non-metric multidimensional scaling ordination plots (MDS) were produced to visualize
8 multivariate patterns of polychaete assemblages classified at species, genus, family and order
9 taxonomic rank. All plots were based on Bray Curtis similarity matrix of untransformed data.
10 A similarity percentage (SIMPER) routine was performed to detect the species most responsible for
11 differences in the multivariate structure of assemblages between periods.
12 A second-stage nMDS ordination was also plotted to visualize differences among similarity
13 matrices at different levels of taxonomic aggregation and data transformation (Sommerfield and
14 Clarke, 1995).
15 All multivariate analyses were performed using the computer program PRIMER v6 (Clarke and
16 Gorley, 2006), including the add-on package PERMANOVA+ (Anderson et al., 2008).

17

18 **3. Results**

19

20 **3.1. Faunal composition**

21 A total of 5680 polychaete specimens belonging to 173 species, 115 genera, 35 families and 14
22 orders were collected: among them, 2941 individuals (belonging to 94 species, 67 genera, 29
23 families and 12 orders) were collected during the first period (1990-1994), and 2739 (130 species,
24 95 genera, 35 families and 14 orders) during the second one (2004-2008).

25 As far as the species abundances are concerned, during the first period *Owenia fusiformis* ranked
26 first (21.2 % of the individuals) followed by *Pectinaria auricoma* (15.4 %), *Eunice vittata* (13.1 %) and
27 *Nothria conchilega* (10 %). No other species exceeded the 5 % of the total abundance. During
28 the second period *O. fusiformis* remained the most abundant species (10.7 %), but 3 species showed
29 similar abundances, namely *Ampharete acutifrons* (10.1 %) (not recorded during 1990-1994),
30 *Notomastus latericeus* (9.9 %) and *P. auricoma* (9.7 %). Among the other species only
31 *Galathowenia oculata* (6.6 %) exceeded the 5 % of the total abundance. As a whole, 39 singletons
32 (i.e. species represented by a single individual) were recorded, among them 12 during the first
33 period (1 at station 005, 4 at 007, 7 at 107) and 17 during the second one (6 at station 005, 9 at 007,
34 12 at 107). Considering the genera, 24 were singletons, among them 9 during the first period (3 at

1 007, 6 at 107) and 15 during the second one (1 at station 005, 7 at 007, 7 at 107). No singleton
2 families and orders were observed.

3 The distribution of individuals was variable during the first period (1990-1994) both considering the
4 three stations and the four sampling times (Fig. 2); a lesser degree of variation was visible during
5 the second period (2004-2008). The species richness (Fig. 2) was generally the lowest at the station
6 5 during the first period and particularly variable during time 2 (period 1) at stations 7 and 107;
7 during the second period, the species richness showed a temporal trend variable within each station
8 but quite similar among stations. The Simpson diversity index (Fig. 2) showed similar trends at all
9 stations; this index appeared more variable, tending to increase from time 1 to time 4 during the first
10 period, while it appeared more homogeneous among times and stations during the second one.

11 The ANOVA test (Table 1) confirmed the high degree of spatial and temporal variation of the
12 polychaete abundance at the 3 stations during the two analyzed periods; particularly, the
13 significance of the $T(\text{Pe}) \times \text{St}$ interaction term in the analysis of the number of individuals, revealed
14 that the polychaete abundance varied among times depending on the considered station without a
15 clear pattern between the two considered periods. The test for the species richness indicated
16 significant differences among times and stations, but no difference between periods. The analyses
17 of Simpson diversity revealed significant differences between the polychaete assemblages sampled
18 during 1990-1994 and those sampled during 2004-2008; the test also indicated significant
19 differences among times and stations.

20

21 **3.2. Multivariate Analyses**

22 The results of the MDS analyses carried out on the untransformed abundance species matrix and on
23 matrices derived from the aggregation of species distributions to genus, family and order levels are
24 shown in Figure 3. The plot relative to the polychaete assemblages analyzed at species level (Fig.
25 3a) showed that centroids representing the 5 times for each of the 3 station sampled during 2004-
26 2008 (full triangles on the right) formed a group apart from those representing the 4 times for the
27 same stations for the period 1990-1994, thus confirming differences between periods already
28 observed for the univariate indices (Table 1). Almost identical positions of the centroids in the plot
29 were observed using the genera as surrogates of the species (Fig. 3b). The multivariate pattern
30 remained clearly visible when the polychaete assemblage was analyzed at family (Fig. 3c) and order
31 level (Fig. 3d), although the separation between periods became less evident.

32 The species contributing to the 70% dissimilarity between the two periods (Average dissimilarity
33 79.82), and their average abundance in both periods are shown in Table 2 (SIMPER test). The
34 species mostly contributing to differentiate the two periods were also the species dominating the

1 assemblages (see 3.1). Interestingly, among the co-familial species only those belonging to
2 Flabelligeridae (2 species) and Pectinariidae (2) showed similar trend of average abundance
3 between the two periods, while species belonging to Onuphidae (3), Oweniidae (2), Spionidae (2)
4 and Ampharetidae (2) showed opposite temporal trends.

5 Table 3 shows the outcomes of the PERMANOVA tests carried out on the original, untransformed
6 species matrix and on matrices derived from the aggregation of species distributions to genus,
7 family and order level. A large degree of variation characterized the polychaete assemblages at all
8 the considered taxonomic levels. The four tests indicate the significance of the $T(\text{Pe}) \times \text{St}$
9 interaction term revealing that, whatever the analyzed taxonomic level, the polychaete assemblages
10 varied among times depending on the considered station without a clear pattern, even between
11 periods.

12 Considering the estimate of the variance components (Table 3) however, some difference
13 characterized the analyzed datasets: apart from the residuals, the major source of variation belonged
14 to the factor period for the assemblages analyzed at species and genus level, while for the same
15 assemblages analyzed at family and order level the major source of variation belonged to the $T(\text{Pe})$
16 $\times \text{St}$ interaction term. Also, the total variation appeared to decrease with the increasing taxonomic
17 level; this pattern was particularly evident when the assemblages were analyzed at family and order
18 level.

19 Figure 4 compares the relative estimates of the variance components of the untransformed datasets
20 (species, genus, family and order) (Fig. 4a), to those obtained after square-root (Fig. 4b), fourth-root
21 (Fig. 4c) and presence/absence (Fig. 4d) data transform. In every case, the largest variation was
22 among replicate units (i.e. Residual term), while, apart from the analysis of the untransformed
23 datasets at family and order level, the second largest source of variation was always associated to
24 the factor period whatever the taxonomic level and the data transformation used.

25 The ordination of similarity matrices in the second-stage nMDS plot (Fig. 5) showed a typical 'fan'
26 pattern, with a vertical and horizontal spread of points at increasing data transformation and
27 taxonomic aggregation respectively, indicating independent effects of transformations and
28 taxonomic resolution. The effect of taxonomic resolution was particularly evident moving from
29 genus to family level, while the effect of data transformation was already noticeable using the
30 weakest 2nd root transformation because the similarity matrix based on untransformed data fall apart
31 from those obtained by data transformation independently from the taxonomic level considered. In
32 general, within the matrices relative to the same taxonomic rank, those derived from each
33 transformation tend to cluster apart from the similarity matrix obtained by untransformed data.

34

1 4. Discussion

2

3 As well summarized by the univariate indices, a large and significant degree of variation
4 characterizes the analyzed polychaete assemblages both spatially, at the three stations, and
5 temporally, considering the two analyzed time scales.

6 Differences between the two periods were visible by the nMDS plot relative to the species showing
7 separation among the centroids representing the assemblages sampled during the 1990-1994 post
8 anoxic period and those sampled two decades later (2004-2008). This seems to confirm temporal
9 changes in the polychaete assemblages possibly due to recovery from anoxia. Also in another area
10 of the NA, Stachowitsch and Fuchs (1995) observed that the recovery of the macrobenthic
11 community after the mass mortality is not reached even ten years after the anoxic event, suggesting
12 that dramatic events might influence assemblages for decades.

13 PERMANOVA tests confirmed the high spatial-temporal variation as a proper characteristic of the
14 analyzed polychaete assemblages. The main results of differences in assemblages between periods
15 were consistent whatever the considered taxonomic level. However, the describing efficiency of
16 surrogates showed differences concerning the capability to properly describe the assemblages'
17 intrinsic variability. This should not be underrated due to the importance of variability in describing
18 the analyzed assemblages.

19 Particularly, when untransformed data were considered, the use of families and orders as species
20 surrogates led to misinterpreting the sources of assemblage variation and to noticeable decreasing
21 the estimate of the total variation thus allowing considering the two period and the three stations
22 more similar to each other that they really are. In general, it might be expected that using TS (i.e. a
23 lesser number of variables) leads to reduce the explicated variability, but this "averaging effect"
24 (De Biasi et al., 2003; Doak et al., 1998) is not necessarily the rule (see Tataranni et al., 2009). The
25 question is to determine the extent to which this reduction is acceptable, that is, the amount of
26 variability that can be lost without losing the capability to highlight differences among
27 assemblages. If the pattern of community change is marked, interpretable results are possible
28 independent of both the examined component of the benthos and the taxonomic level at which the
29 analyses are carried out (Somerfield and Clarke, 1995). Anyway, evidences suggest that using TS
30 might cause a significant loss of information when differences among assemblages are not robust
31 enough (Musco et al., 2009). The decrease of explicated variability might also result from not
32 concordant distribution patterns of taxonomically related species that show differential response to
33 the stressor (Musco et al., 2009). Several co-familial species showed opposite abundance patterns
34 between the two periods (see 3.2, results of SIMPER). The loss of information observed in the

1 MDS plots based on family and order taxonomic ranks should be carefully considered. The
2 presence of dominant species belonging to the same genus (or family in this case) showing different
3 responses to a perturbation is considered one of the most important factor limiting the efficiency of
4 the TS method (Dauvin et al., 2003).

5 Interestingly, weak data transformation was sufficient to allow perfect correspondence in the
6 estimate of variance components among species and taxonomic surrogates. This clearly indicates
7 that abundance is a key factor characterizing the polychaete assemblages. The importance of
8 abundance was further confirmed by the 2nd stage MDS plot, which however indicated that the
9 similarity among matrices rapidly declined after data transformations, independently from the
10 analyzed taxonomic level. This also recommends care in the choice of data transformations.

11 This study indicates that untransformed data at family level (the most common taxonomic surrogate
12 in environmental monitoring) may represent appropriate assemblages' descriptors in long-term
13 monitoring studies (Bevilacqua et al., 2010; Lasiak, 2003; Olsgard et al., 1998; Wlodarska-
14 Kuwalczuk and Kedra, 2007). Our results are in accordance with Bevilacqua et al. (2009)
15 suggesting that, in the absence of previous acknowledgements, untransformed data should be
16 analyzed, since it is often difficult to recognize a priori how environmental variations will affect
17 assemblages' structure (e.g., influencing rare or abundant species).

18 Our data also suggest that, before applying TS and perform approximations of the faunal features of
19 an area, the species-level information should be achieved (Fraser et al., 2006; Gage, 2001; Musco et
20 al., 2009; Olsgard and Somerfield, 2000; Terlizzi et al., 2003). Moreover, as argued by Tataranni et
21 al. (2009), our data support that periodical analysis at fine taxonomic level should be alternated to
22 long-term routine monitoring based on TS, since shifts in dominance between taxonomically related
23 species may occur gradually, altering competitive interactions. This would be particularly alarming
24 if changes in species dominance result from events that are detected only by analyses at the finest
25 taxonomic level, such as alien invasions (see Zenetos et al., 2008) or meridionalization of the NA
26 fauna (Bianchi, 2007; Boero et al., 2008; Mikac and Musco, 2010; Musco and Giangrande, 2005).
27 Changes in community composition over the long trend make up the history of ecosystems and are
28 inherently "unpredictable" (Boero, 1996, 2009, see also Doak et al., 2008). Programming
29 environmental long-term monitoring exclusively based on TS implicitly "predicts" families (higher
30 taxa) as locally fixed unchangeable entities, but this prevents from appreciating important changes
31 within the families, or even genera. For instance, among the worst invasive algae of the
32 Mediterranean, *Caulerpa racemosa* and *C. taxifolia*, rank among the 100 worst aliens (Streftaris and
33 Zenetos, 2006), but their presence would pass unnoticed if the genus *Caulerpa* (represented in the
34 Mediterranean by the common *C. prolifera*) would not be investigated at the species level. The case

1 of the genus *Caulerpa* shows that systems evolve (i.e. change) in time and TS is clearly a not good
2 tool to detect this change.

4 **Acknowledgements**

5 Thanks to Nando Boero for invaluable comments. The results of this investigation as well as the
6 work of BM were carried out within the projects “Mechanisms of long-term changes in the Adriatic
7 Sea ecosystem” (project no. 0098111) and “Biodiversity of benthic communities in the Adriatic:
8 natural and human impacts” (project no. 098-0982705-2732) both funded by the Ministry of
9 Science, Education and Sports of the Republic of Croatia. The work of LM, AT and AG has been
10 carried out within the MARBEF Network of Excellence which is funded in the Community’s Sixth
11 Framework Programme (Contract no. GOCE-CT-2003-505446), the E.U. Integrated Project
12 SESAME and the CMCC (Centro Euro-Mediterraneo per i Cambiamenti Climatici).

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1 **Figure Captions**

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3 Figure 1. Study area and position of the three investigated stations

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5 Figure 2. Univariate indices of polychaete assemblages at each station for both periods during the
6 different sampling times. Mean temporal values calculated for each station were also showed as a
7 line

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9 Figure 3. non-metric MDS ordinations of polychaete assemblages based on Bray-Curtis similarity
10 of untransformed data at species (a), genus (b), family (c) and order (d) taxonomic level of
11 identification

12

13 Figure 4. Estimates of variance components for each source of variation as obtained by
14 PERMANOVA analyses performed at all investigated taxonomic levels, with different
15 transformations: no transformation (a), square root (b), fourth root (c) and presence/absence (d).
16 The variability of each term was expressed as a proportion of the total variation

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18 Figure 5. 'second stage' MDS ordination of resemblance matrices derived from species (S), genus
19 (G), family (F) and order (O) untransformed abundance data and several transformations (2rt:
20 square root; 4rt: fourth root; PA: presence/absence)

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Research highlights

- Polychaetes families detect decadal changes in the multivariate assemblages structure
- TS and data transformation may underrate patterns of spatial assemblages variability
- TS-based long-term monitoring must include periodical fine taxonomic analyses

Table 1. Results of ANOVA analyses for number of individuals, species richness and Simpson diversity testing for differences in polychaete assemblages. P = period; St = station; T = time. Significant P-values are given in italics.

Source	df	Number of individuals			Species richness			Simpson diversity		
		MS	F	P	MS	F	P	MS	F	P
Pe	1	12687	2.66	0.111	228.78	1.83	0.214	0.1751	5.27	<i>0.030</i>
St	2	1112.3	1.06	0.395	163.05	11.07	<i>0.002</i>	0.0219	7.52	<i>0.005</i>
T(Pe)	7	2929.9	2.74	<i>0.046</i>	86.01	5.86	<i>0.003</i>	0.0281	9.70	<i>0.001</i>
Pe × St	2	2299.7	2.19	0.136	49.031	3.33	0.067	0.0063	2.16	0.166
T(Pe) × St	14	1069.2	3.49	<i>0.001</i>	14.665	0.85	0.630	0.0029	0.95	0.530
Res	86	306.47			17.344			0.0031		

Table 2. Results of SIMPER analysis. Average abundance (Av. Abund.) and percentage contribution (Contrib. %) to the average dissimilarity between periods for species reaching the cumulative contribution of 70% are reported. Species are divided in relation to the family and order taxonomical levels, which are listed alphabetically

Order	Family	Species	Period 1	Period 2	Contrib%
			Av. Abund	Av. Abund	
Capitellida	Capitellidae	<i>Notomastus latericeus</i>	2.43	4.11	4.92
Eunicida	Eunicidae	<i>Eunice vittata</i>	8.19	0.77	7.99
	Lumbrineridae	<i>Lumbrineris latreilli</i>	1.51	0	2.06
	Onuphidae	<i>Nothria conchilega</i>	6.28	0.09	6.35
		<i>Aponuphis grubii</i>	0	1.2	1.51
		<i>Aponuphis brementi</i>	0.96	0.73	1.4
Flabelligerida	Flabelligeridae	<i>Pherusa plumosa</i>	0.96	0.05	1.18
		<i>Piromis eruca</i>	0.85	0.03	1
Oweniida	Oweniidae	<i>Owenia fusiformis</i>	13.26	4.42	12.99
		<i>Galathowenia oculata</i>	0.38	2.73	3.46
Phyllodocida	Glyceridae	<i>Glycera unicornis</i>	1.04	0.74	1.5
Sabellida	Serpulidae	<i>Pomatoceros triqueter</i>	0.23	0.89	1.27
Spionida	Spionidae	<i>Polydora ciliata</i>	1.68	0	1.82
		<i>Spiophanes kroyeri</i>	0	1.21	1.66
Sternaspida	Sternaspidae	<i>Sternaspis scutata</i>	0.23	1.3	1.72
Terebellida	Ampharetidae	<i>Ampharete acutifrons</i>	0	4.2	5.34
		<i>Amphicteis gunneri</i>	2.47	0.2	2.75
	Pectinariidae	<i>Pectinaria auricoma</i>	9.66	4.03	9.15
		<i>Pectinaria koreni</i>	0.96	0.38	1.44
	Trichobranchidae		<i>Terebellides stroemi</i>	0.11	1.09

Table 3. PERMANOVA analyses based on the Bray-Curtis dissimilarity for untransformed abundance data at species (173 variables), genera (115), family (35) and order (14) taxonomic level. The analyses were carried out using 999 permutations of residuals under a reduced model. Estimates of variance components (VC) for each analysed source of variation were also included. P = period; St = station; T = time

Source	df	Species				Genera			
		MS	F	P(perm)	VC	MS	F	P(perm)	VC
Pe	1	56099	3.81	0.006	798.78	54286	3.98	0.007	783.09
St	2	11372	3.98	0.001	234.55	11143	4.21	0.001	234.02
T(Pe)	7	6965.8	2.41	0.001	325.09	6644.1	2.48	0.001	316.35
Pe × St	2	8643.2	3.02	0.001	318.75	7791.2	2.94	0.001	283.36
T(Pe) × St	14	2893.4	2.07	0.001	358.36	2681.2	2.08	0.001	333.44
Res	86	1395.5			1395.	1287.4			1287.4
Tot	112				3431.03				3237.66

Source	df	Families				Orders			
		MS	F	P(perm)	VC	MS	F	P(perm)	VC
Pe	1	25183	2.23	0.031	278.61	15721	2.06	0.039	164.61
St	2	9606.8	4.13	0.001	200.61	6880.3	4.12	0.001	143.51
T(Pe)	7	6019.1	2.55	0.001	292.32	3490	2.06	0.002	143.09
P × St	2	6440.4	2.77	0.001	226.74	5009.8	2.99	0.002	183.95
T(Pe) × St	14	2357.2	2.37	0.001	325.69	1697.8	3.02	0.001	271.64
Res	86	995.83			995.83	562.38			562.38
Tot	112				2319.08				1469.18

