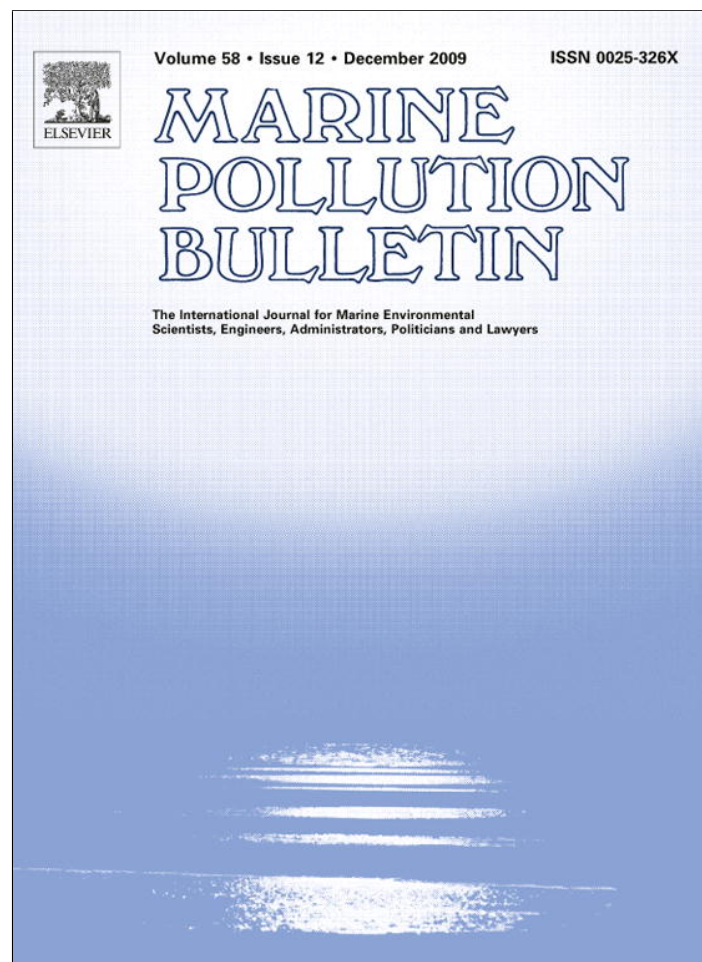


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Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Taxonomic sufficiency in the detection of natural and human-induced changes in marine assemblages: A comparison of habitats and taxonomic groups

Stanislao Bevilacqua*, Simonetta Frascchetti, Luigi Musco, Antonio Terlizzi

Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali, Università del Salento, Lecce, CoNISMa, I-73100 Lecce, Italy

ARTICLE INFO

Keywords:

Taxonomic surrogates
Human impacts
Environmental gradients
Mollusks
Polychaetes
Multivariate analyses

ABSTRACT

Taxonomic Sufficiency (TS) is a promising analysis technique, particularly in light of the current need for rapid and reliable procedures in marine impact assessment and monitoring. However, generalizations are still difficult and there are few studies comparing the effectiveness of TS under different environmental settings. The present study investigates whether reduced taxonomy can be used to detect natural and human-driven patterns of variation in mollusk and polychaete assemblages from subtidal soft and hard bottoms in the Mediterranean. Results showed that, unlike in polychaetes, mollusk families represent effective taxonomic surrogates across a range of environmental contexts. These findings suggest that the mechanisms behind TS in mollusks could act homogeneously across habitats and environmental conditions. In contrast, multiple factors could interact to determine the robustness of polychaetes to taxonomic aggregation. This study highlights the need to go beyond the current pragmatism in this field of work and focus on the reasons underlying TS effectiveness in order to provide a general framework on the application of taxonomic surrogates in marine systems.

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1. Introduction

As anthropogenic disturbances in marine systems have increased rapidly and dramatically worldwide in recent decades (Halpern et al., 2008), the development of fast and cost-effective procedures for impact assessment and monitoring has become a pressing issue for marine ecologists (Warwick, 1993; Bell et al., 2006). In this context, the concept of Taxonomic Sufficiency (TS; Ellis, 1985) has been receiving increasing attention in recent years. The basic concept of TS is that anthropogenic impacts can be detected using coarse taxonomic resolutions without a significant loss of information, thus avoiding long and difficult precise taxonomic identifications and saving time and costs (Olsgard and Somerfield, 2000). This concept is based on the principle that the effects of an environmental stress could propagate up through the taxonomic hierarchy as its magnitude increases (Pearson and Rosenberg, 1978; Ferraro and Cole, 1990), causing noticeable variation in assemblage structure above the species level. It has also been suggested that higher taxa may reflect the effect of human disturbance even better than species, with the latter being more sensitive to the confounding influence of natural environmental variation (Warwick 1988a, 1988b; Vanderklift et al., 1996).

Although TS has also been adopted in conservation studies in marine systems (Vanderklift et al., 1998; Bates et al., 2007), it

has mainly been applied in the assessment of environmental impacts. When lumping species abundance into higher taxonomic ranks, the effects of anthropogenic disturbance on assemblage structure have been clearly detected at the genus or family level (e.g., Gomez Gesteira et al., 2003) and, in some cases, even at the phylum level (e.g., Defeo and Lercari, 2004). However, several authors have pointed out that differences in assemblage structure among impacted and reference conditions are generally less evident when using a decreasing level of taxonomic resolution (Somerfield and Clarke 1995; Olsgard et al., 1998), whereas the opposite has been rarely documented (but see Smith and Simpson, 1993).

Currently, it is commonly acknowledged that family-level identification may be sufficient to examine variation in marine assemblages exposed to environmental impacts in routine monitoring programs (e.g., Somerfield and Clarke, 1995; Olsgard et al., 1998; Gomez Gesteira et al., 2003; Thompson et al., 2003; Lampadariou et al., 2005). Family is also likely to be a good predictor of species-level variation related to natural environmental gradients (De Biasi et al., 2003; Dethier and Schoch, 2006). However, it is still difficult to make generalizations regarding predictors of variation. The use of taxonomic surrogates in investigating patterns of assemblage variation along natural gradients still remains substantially unexplored (Włodarska-Kowalczyk and Kędra, 2007). In impact assessment, the application of TS has focused on strong pollution gradients, mostly including oil and heavy metal pollution (see Dauvin et al., 2003 for a review). The use of coarser taxonomic resolution in the analysis of weak or intermediate human threats

* Corresponding author. Tel.: +39 0832 298853; fax: +39 0832 298702.
E-mail address: stanislao.bevilacqua@unisalento.it (S. Bevilacqua).

has largely been disregarded. Most studies have examined soft bottom benthic assemblages in the North Atlantic in relation to oil pollution gradients (Herman and Heip, 1988; Warwick 1988a,b; Somerfield and Clarke, 1995; Olsgard et al., 1998; Olsgard and Somerfield, 2000). Fewer attempts have been made to test TS in other geographic contexts or in habitat types such as tropical areas (Torres Mendes et al., 2007) or rocky shores (Lasiak, 2003).

The major risk in the use of TS is that the potential loss of information related to the decreased taxonomic detail could be underestimated, especially in poorly known systems or when pilot studies on the application of this technique are not available (Chapman, 1998; Narayanaswamy et al., 2003; Quijón and Snelgrove, 2006). Reduced taxonomic information could restrict inferences about the causality of observed patterns (Defeo and Lercari, 2004), or could fail to highlight the subtle effects of environmental stress on assemblage structure. For instance, low taxonomic resolution could reduce differences in the multivariate structure of assemblages between impacted areas and controls (Somerfield and Clarke, 1995; Vanderklift et al., 1996; Pagola-Carte et al., 2002), and the loss of information could be even more severe when low taxonomic detail is coupled with strong data transformations (Olsgard et al., 1997).

The sufficient level of taxonomic resolution could be strongly context-dependent (Terlizzi et al., 2003a) and could change according to the bio-geographic background (Roy et al., 1996) or the habitat type (Chapman, 1998) or due to different relationships of abundance and redundancy among species. Since the degree of taxonomic relatedness of species differs among phyla (Warwick and Somerfield, 2008), the ability of higher taxa to reflect species-level variation could also vary depending on the type of organisms involved (Vanderklift et al., 1998; Hirst, 2006). To date, the application of TS to single taxonomic groups is scarce, even for those groups widely employed in marine environmental benthic monitoring such as mollusks (Terlizzi et al., 2005a; Torres Mendes et al., 2007) or polychaetes (Giangrande et al., 2005; Domínguez-Castanedo et al., 2007). TS studies have generally focused at the assemblage level, and have included different groups of organisms. However, changes in phylogenetic ranking among phyla make conclusions based on taxonomic relationships more stringent when applied to a single phylum than to all phyla combined (Ellingsen et al., 2005). Moreover, the success of taxonomic surrogates could rely on mechanisms such as the numerical correlation among species and higher taxa, potential relationships between functional and taxonomic diversity, and different responses to human disturbance, which could be strongly group-dependent. The application of TS to whole assemblages, although of great interest from a practical point of view, could hide basic explanations for the suitability of taxonomic surrogates. In this light, studies comparing variation in the taxonomic sufficient level among different organisms, habitats and/or environmental conditions would also be of great help to building a general conceptual framework for the application of TS. The responses to reduced taxonomic resolution for detecting natural and human-driven patterns of variation have been tested in mollusk and polychaete assemblages from subtidal soft and hard bottoms. We examined eight existing data sets from previous studies on the effects of human impacts or natural environmental gradients on distributional patterns of assemblages in the Mediterranean. Specifically, we compared the effects of taxonomic aggregation on the analysis of multivariate patterns of assemblage variation related to natural gradients and human impacts among considered habitats and organism types. This allowed us to assess whether (1) the degree of sufficient taxonomic resolution varies between organisms and/or habitats; and (2) impacts produce patterns of variation in assemblage structure that are more robust to TS than natural environmental gradients.

2. Methods

2.1. Datasets

A total of eight data sets from Mediterranean benthic assemblages under different ecological and biological settings were analyzed. Datasets were chosen because both groups showed significant differences in the structure of mollusk and polychaete assemblages at the species level between impacted and control locations or along environmental gradients, and because they referred exactly to the same sources of anthropogenic disturbance and natural gradients. A detailed description of the data sets is reported in Table 1.

Four data sets were derived from a study on the effects of offshore gas production platforms on soft bottom macro-benthic assemblages in the Ionian Sea (SW Italy; Terlizzi et al., 2008). Sampling was carried out at increasing distances from platforms (300, 1000, and 3000 m) from five sites randomly selected within each distance (Fig. 1a), with three 0.1 m² van Veen grabs in each site, sieved using 1-mm mesh. Two data sets, referred to as 'Molluscs LB' and 'Polychaetes LB', were collected close to platform LB and were considered to be examples of anthropogenic disturbance in soft bottom habitats. The other two data sets, 'Molluscs SB' and 'Polychaetes SB', were obtained using data from areas that were not impacted by the platform (i.e., sites at 3000 m from platforms; see Terlizzi et al., 2008). Since non-impacted sites were positioned within two different depth ranges (i.e., 20–40 m and 70–90 m) at two locations within each range, only a subset of the three sites lying at approximately the same depth were selected for each location to avoid confounding the variability among sites or locations with within-depth range variability. We analyzed samples taken on soft bottoms at 30 m and 90 m, in two locations for each depth and at three sites within each location (Fig. 1b), with three 0.1 m² van Veen grabs in each site. These two data sets were analyzed here as examples of natural depth gradients in soft bottoms habitats.

Two other data sets were taken from studies investigating the impact of sewage discharge on mollusk (Terlizzi et al., 2005a) and polychaete assemblages (Musco et al., 2009) in subtidal rocky reefs (Ionian Sea, SE Italy), and were indicated as 'Molluscs OF' and 'Polychaetes OF', respectively. For both studies, sampling was undertaken in the impacted location (I) and in two control locations (C1 and C2, hereafter indicated together as Cs; Fig. 1c), with three sample sites within the locations and nine replicates per site. These two data sets were reported as cases of impacts in hard bottom habitats.

The last two data sets, 'Molluscs HB' and 'Polychaetes HB', were taken from two studies exploring spatial patterns of distribution of mollusk (Terlizzi et al., 2003b) and polychaete (Giangrande et al., 2003) assemblages, respectively, along a depth gradient in subtidal rocky cliffs (Adriatic Sea, SE Italy; Fig. 1d). Sampling was carried

Table 1

Number of samples, species, and individuals for each data set considered in the study. For data sets derived from larger studies including other macrofaunal groups, the percentage on the total number of species and individuals accounted for mollusks and polychaetes are given in brackets.

Data set	No. of sample	No. of species	No. of individuals
Molluscs LB	45	157(60)	3625 (74)
Polychaetes LB	45	45 (17)	748 (15)
Molluscs OF	81	151	5707
Polychaetes OF	81	106	5908
Molluscs SB	36	105 (45)	1201 (32)
Polychaetes SB	36	77 (33)	1313 (35)
Molluscs HB	27	94	2878
Polychaetes HB	27	95	1634

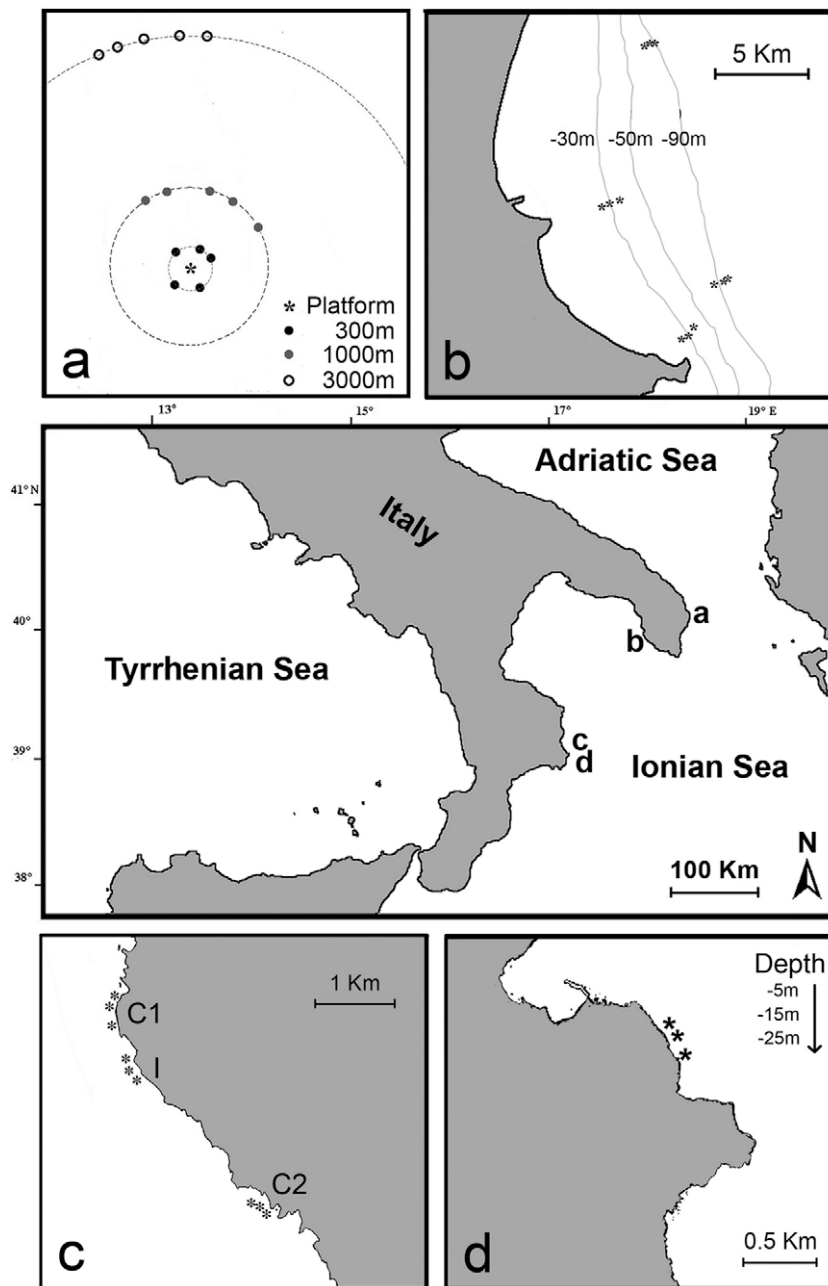


Fig. 1. Map of study locations. (a) The offshore gas platform, LB, and the locations of sites at increasing distances from the platform (LB data sets); (b) Locations and (*) nested sites at -30 m and -90 m (SB data sets); (c) Sewage outfall (I) and control (C1, C2) locations, with (*) nested sites (OF data sets); and (d) Sites investigated at different depths (HB data sets).

out in three sites at three different depths (i.e. 5, 15, and 25 m) for each site, with three replicates per site. These two data sets were representative of natural depth gradients in hard bottom habitats.

2.2. Statistical analyses

Distance-based permutational multivariate analyses of variance (PERMANOVA; Anderson, 2001; McArdle and Anderson, 2001) were employed to test for differences in assemblages among impacted and reference conditions or along natural environmental gradients (i.e., at the three distances from platform for LB data sets, the two depths for SB data sets, the outfall location and the two controls for OF data sets, and the three depths for HB data sets). For LB data sets, the design consisted of two factors: Distance (D,

fixed, three levels) and Site (Si, random, five levels, nested in D), with $n = 3$. For SB data sets, the design was three-factorial, with Depth (De, fixed, 2 levels), Location (Lo, random, 2 levels, nested in De), and Site (Si, random, 3 levels, nested in Lo(De)) as factors and with $n = 3$. For OF data sets, the design was asymmetrical and involved two factors: Location (Lo, with one impacted and two control locations) and Site (Si, random, three levels, nested in Lo), with $n = 9$. In this case, denominators for F ratios were identified following beyond-BACI designs, but tests of terms that involved sources of variation specific for I or Cs were constructed using the natural denominator for that term, not the pooled denominator (Terlizzi et al., 2005b). For HB data sets, the design consisted of two factors: Depth (De, fixed, three levels) and Site (Si, random, three levels, crossed). All analyses were based on

Bray-Curtis dissimilarities calculated on species-level data at different transformations (i.e., untransformed data, square root, fourth root, and presence/absence transformations) and each term of the analysis was tested using 4999 random permutations of appropriate units (Anderson and ter Braak, 2003). For LB and HB data sets, significant terms relevant to hypotheses were investigated using *a posteriori* pair-wise comparisons with the PERMANOVA *t* statistic and 999 permutations. In order to test the robustness of the observed patterns at a decreasing taxonomic resolution, analyses were repeated by aggregating species-level data into higher taxonomic ranks (i.e., from genus to class for mollusks, and from genus to order for polychaetes).

For each data set, a second-stage nMDS ordination was plotted to visualize differences among similarity matrices at different levels of taxonomic aggregation and data transformation (Sommerfield and Clarke, 1995). The RELATE procedure (Clarke and Warwick, 1994) was also employed to calculate the Spearman's correlation coefficient (ρ) between the species similarity matrix and the similarity matrices at higher taxonomic levels (untransformed data), in order to quantify the loss of information generated by aggregating species-level data into higher taxonomic ranks. A third-stage nMDS ordination (Arvanitidis et al., 2009) was also plotted to display how patterns of correlations among similarity matrices at different taxonomic levels change across environmental conditions, habitats and type of organisms. In this procedure, the nMDS ordination was based on the triangular matrix obtained by calculating Spearman's rank correlations between each pair of second-stage triangular matrices. All analyses were conducted using the PRIMER v6 computer with the add-on package PERMANOVA+ (Anderson and Gorley, 2008).

Since the number of higher taxa virtually decreases at increasing taxonomic ranks and such a decrease could also vary among phyla, taxonomic aggregation is likely to assume different meanings depending on the taxonomic rank considered (e.g., genus, family) and/or the group of organisms. To quantify this aspect of taxonomic aggregation, the ratio of the number of higher taxa (N_H) to the total number of species belonging to these taxa (N_S) was calculated for all taxonomic ranks in all data sets. The Pearson's product-moment correlation coefficient (r) was determined to check for any possible correlation between the N_H/N_S ratio and the corresponding ρ values overall in mollusk and polychaete assemblages. For both groups of organisms, ρ values were plotted against the corresponding N_H/N_S ratios. A regression analysis was then carried out, following a step-wise backward selection of the best fitting models using the AIC (An Information Criterion; Akaike, 1974) procedure. Such analyses were conducted using the R statistic software.

3. Results

Results of PERMANOVAs carried out at different levels of taxonomic resolution and data transformation on all data sets are summarized in Table 2. For 'Molluscs LB', PERMANOVA at the species level highlighted significant differences ($P < 0.001$) in mollusk assemblages at increasing distances from the offshore gas platform. Pair-wise comparisons revealed that assemblages differed among the platforms at all distances, a result that was similar to results observed for the whole benthic assemblage (see Terlizzi et al., 2008). The analyses showed that this pattern of assemblage variation was retained up to the order level, independent of data transformation. At the class level, though with a higher P value ($P < 0.05$), differences among distances were still significant at all transformations and results of pair-wise comparisons did not match those observed at other levels of taxonomic resolution. For 'Polychaetes LB', analyses on untransformed data showed significant differences ($P < 0.01$) in assemblages among distances, from

species to orders. Such differences were still significant at all investigated taxonomic levels when data were transformed, although P -values generally decreased (up to $P < 0.05$) with increases in data transformation. Pair-wise comparisons on untransformed species data showed that polychaete assemblages at 300 m differed from those at 1000 m and 3000 m, while those at 1000 m and 3000 m were not significantly different. This pattern was consistent at all taxonomic levels and transformations, except for family and order with untransformed data. Polychaete assemblages at 300 m and 1000 m did not differ between family and order, and assemblages at both 300 m and 1000 m differed from those at 3000 m.

For 'Molluscs OF', the PERMANOVA on species-level data showed significant differences in mollusk assemblages between the impacted versus control locations (*I-v-Cs*) at all transformations, even though P -values increased as stronger data transformations were used. Similar results were observed at the genus and family level, where *I-v-Cs* was not significant using presence-absence data. At the order and class level, only analyses on untransformed data revealed significant differences for *I-v-Cs*. In the case of 'Polychaetes OF', analyses on untransformed data showed significant differences for *I-v-Cs* at all taxonomic levels. When mild levels of data transformation (i.e., square and fourth root transformations) were applied, such differences in polychaete assemblages were still significant at all taxonomic levels, with the exception of families, where the contrast *I-v-Cs* was not significant. Analyses on presence-absence data showed a significant *I-v-Cs* contrast only at the genus level.

For 'Molluscs SB', the PERMANOVA showed that assemblages vary significantly between the two depths up to the family level, independent of data transformation. P -values generally increased when species were aggregated into higher taxonomic ranks, and became non-significant for order and class data. For 'Polychaetes SB', analyses produced similar results. Compared with mollusks, however, PERMANOVA highlighted a stronger effect of taxonomic aggregation, showing significant variation between the two depths for all transformations at only the species and genus levels. At the family level, significant differences between the distances were identified only with mildly transformed data, though P -values were very close to the limit of significance. No differences between depths were observed at the order level.

For 'Molluscs HB', a PERMANOVA of species- and genus-level data showed significant variation in mollusk assemblages along the depth gradient, with assemblages at 5 m differing strongly from those at 15 and 25 m, which, in turn, were not significantly different. For species and genus data, transformations did not have a significant effect on the outcomes of analyses. Patterns of assemblage variation identified at the family level were only consistent with those at the species and genus levels for untransformed and presence-absence data. At the order and class level, differences in assemblages along the depth gradient were not significant or, where significant, produced patterns that were not interpretable in relation to depth. For 'Polychaetes HB', a PERMANOVA on untransformed data at the species and genus level showed significant variation in assemblages along the depth gradient, with shallow assemblages differing strongly from those at higher depths. Such differences, though still significant, were no more clearly interpretable when data were transformed. Differences among depths were always non-significant at the family and order levels.

The ordination of similarity matrices in second-stage nMDS plots (Fig. 2) showed a typical 'fan' pattern for each investigated data set, with a vertical and horizontal spread of points at increasing data transformation and taxonomic aggregation respectively, indicating that the effects of transformations and taxonomic resolution operated independently. The effect of transformations, however, varied across different environmental conditions and habitat types, mostly affecting differences among similarity matrices at a

Table 2
Summary of PERMANOVAs testing for differences related to human impacts or along natural gradients in mollusk and polychaete assemblages from soft and hard bottom habitats (see details in the text), carried out at different levels of taxonomic resolution and data transformation. Analyses were based on Bray–Curtis dissimilarities and each test was performed using 4999 permutations of appropriate units. Only tests for the terms relevant to hypothesis have been reported. *P*-values were obtained using 4999 Monte Carlo samples from the asymptotic permutation distribution. For LB and HB data sets, significant *P*-values are given in italic when results of associated pair-wise tests (results not showed) differed from those obtained with species level untransformed data. In all other cases significant *P*-values are given in bold.

Environmental context	Habitat type	Impact/gradient type	Data set	Source of variability	Data transformation	Taxonomic resolution				
						Species	Genus	Family	Order	Class
Human impacts	Mud flats	Off-shore gas extraction	Molluscs LB	Distance (D)	None	0.000	0.000	0.000	0.000	<i>0.014</i>
					√	0.000	0.000	0.000	0.000	<i>0.039</i>
					√√	0.000	0.000	0.000	0.000	<i>0.018</i>
			P/A	0.000	0.000	0.000	0.000	<i>0.018</i>		
			Polychaetes LB	Distance (D)	None	0.006	0.005	<i>0.004</i>	<i>0.007</i>	–
					√	0.010	0.006	0.005	0.012	–
	√√	0.017			0.009	0.007	0.017	–		
	P/A	0.021	0.010	0.016	0.033	–				
	Rocky reefs	Sewage discharge	Molluscs OF	<i>I-v-Cs</i>	None	0.000	0.002	0.001	0.009	0.026
					√	0.002	0.006	0.011	0.059	0.054
					√√	0.012	0.044	0.031	0.224	0.131
			P/A	0.042	0.164	0.093	0.679	0.183		
Polychaetes OF			<i>I-v-Cs</i>	None	0.000	0.000	0.000	0.000	–	
				√	0.009	0.000	0.077	0.000	–	
	√√	0.021		0.000	0.142	0.000	–			
P/A	0.059	0.000	0.305	0.128	–					
Natural gradients	Mud flats/sandy detritic	Depth/substrate heterogeneity	Molluscs SB	Depth (De)	None	0.011	0.018	0.024	0.198	0.201
					√	0.009	0.022	0.027	0.239	0.319
					√√	0.005	0.021	0.027	0.250	0.521
			P/A	0.007	0.021	0.022	0.287	0.548		
			Polychaetes SB	Depth (De)	None	0.014	0.029	0.065	0.098	–
					√	0.006	0.015	0.046	0.094	–
					√√	0.005	0.018	0.043	0.102	–
			P/A	0.005	0.016	0.067	0.152	–		
			Rocky cliffs	Depth	Molluscs HB	Depth (De)	None	0.003	0.013	0.019
	√	0.001					0.002	<i>0.003</i>	<i>0.015</i>	0.296
	√√	0.000					0.001	<i>0.003</i>	<i>0.042</i>	0.132
	P/A	0.000			0.002	0.006	0.007	<i>0.047</i>		
	Polychaetes HB	Depth (De)			None	0.002	0.005	0.105	0.247	–
					√	<i>0.001</i>	<i>0.007</i>	0.086	0.404	–
			√√	<i>0.001</i>	<i>0.011</i>	0.117	0.631	–		
	P/A	<i>0.001</i>	<i>0.020</i>	0.184	0.807	–				

None = no transformation; √ = square root; √√ = fourth root; P/A = presence–absence.

varying taxonomic resolution in hard bottom natural gradients (HB data sets), with a less pronounced effect on soft bottom impact data (LB data sets). For mollusk data sets, the ordination plot showed a clear clustering pattern among species-, genus- and family-level matrices, which was more evident in impact cases (Molluscs OF and LB). For polychaetes, similarity matrices were increasingly separated as taxonomic resolution decreased, with minor differences between species and genus matrices. Such patterns were retained for both groups at all transformations applied (Fig. 2), though separation among similarity matrices increased when taxonomic groups became increasingly aggregated as transformations become stronger.

The significantly high values for Spearman's correlation between the species similarity matrix and matrices at the genus and family levels in mollusk data sets (always $\rho > 0.91$, $P < 0.01$) indicated that very little information is lost going from species to families irrespective of the environmental context and/or habitat type (Table 3). A clear drop in the resemblance among matrices of species and higher taxa was observed for orders and classes, even though ρ values were still significant ($P < 0.01$). For polychaete assemblages, in contrast, ρ values among species and matrices for higher taxa (all significant at $P < 0.01$) decreased progressively after the genus level. Polychaete assemblages also exhibited a higher variability among data sets compared to mollusks, with the highest values for SB and the lowest for HB (Table 3). Patterns of variation among data sets indicated by Spearman's

correlations between similarity matrices at different taxonomic levels were clearly displayed in the '3d stage' nMDS plot (Fig. 3). Mollusk centroids were clearly distinct from polychaete centroids, indicating distinct patterns of correlations among similarity matrices at different taxonomic levels between the two groups of organisms. All mollusk data sets clustered together, denoting similar relationships among taxonomic ranks across environmental conditions and/or habitat types. For polychaetes, in contrast, a clear separation between hard and soft bottom data sets emerged, indicating that the way by which information declined across taxonomic levels differed strongly between the two habitats.

The N_H/N_S ratio was strongly correlated with the corresponding ρ values in all cases (for all correlations, $r > 0.70$, $P < 0.001$). For mollusk assemblages, the AIC procedure selected a second-order polynomial model fitting ρ values against the N_H/N_S ratios (adjusted $R^2 = 0.52$, $P < 0.01$; Fig. 4a) whereas for polychaetes, the selected model was linear (adjusted $R^2 = 0.52$, $P < 0.01$; Fig. 4b). At increasing taxonomic levels, mollusks revealed comparable decreasing patterns in the N_H/N_S ratio between soft versus hard bottoms (Fig. 4a), indicating habitat-independent patterns of species distribution within higher taxa. In mollusk assemblages, ρ values remained approximately unvaried up to the family level, despite the reduction in the N_H/N_S ratio (Fig. 4a). At higher taxonomic levels, ρ values decreased progressively with decreasing N_H/N_S ratios. In contrast, for polychaete assemblages, ρ values decreased proportionally with decreasing N_H/N_S ratios, although patterns differed be-

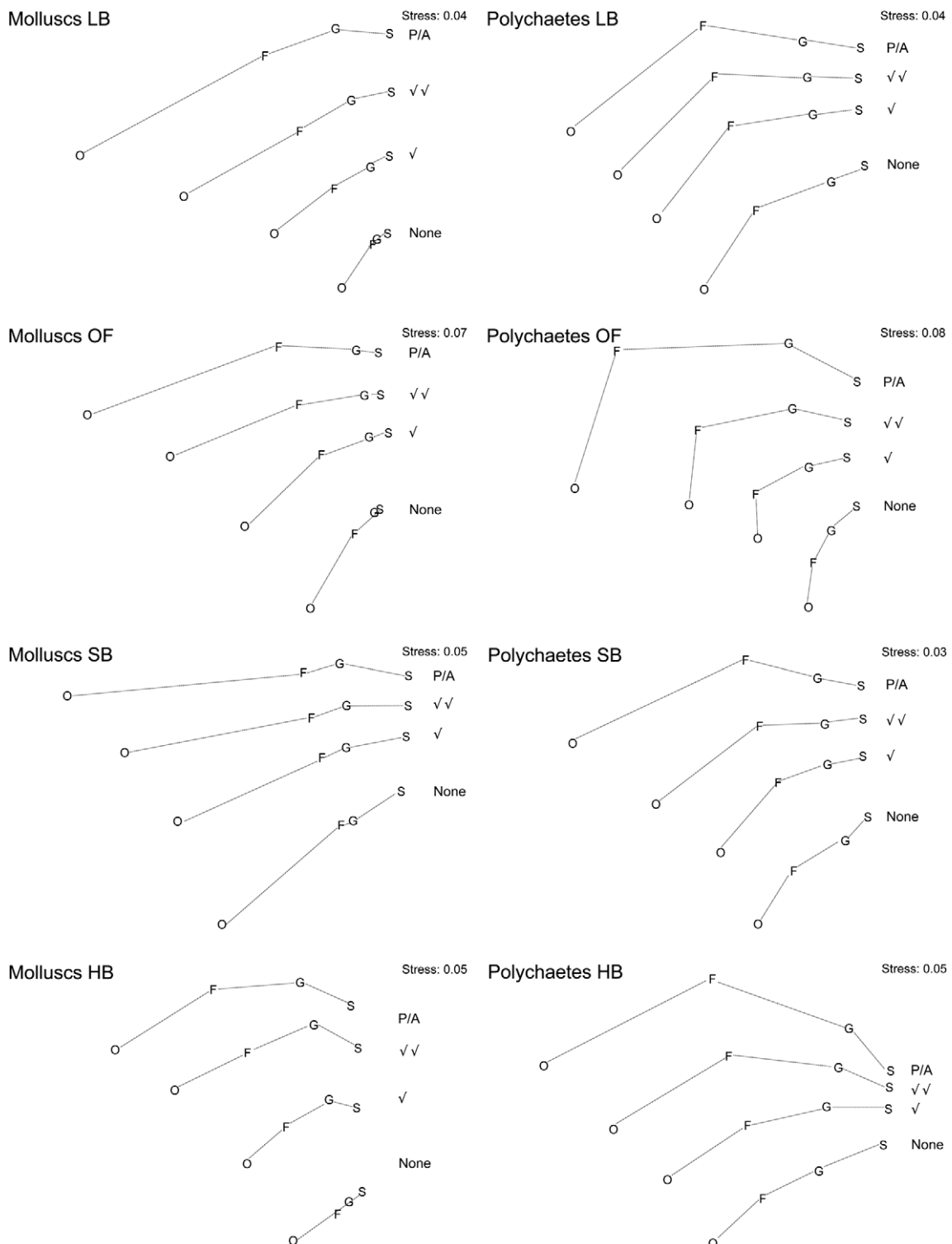


Fig. 2. Second-stage MDS ordination plots of inter-matrix rank correlations for all investigated data sets based on similarity matrices at the species (S), genus (G), family (F), and order (O) level and calculated using different data transformation. The Molluscs' class has been omitted to facilitate comparisons with polychaetes. Lines indicate group matrices with the same level of transformation. None = untransformed, $\sqrt{}$ = square root, $\sqrt{\sqrt{}}$ = fourth root, P/A = presence/absence.

tween the two investigated habitats with a progressively larger decline in hard bottoms than in soft bottoms (Fig. 4b).

4. Discussion

Our findings revealed that mollusk families, and even orders, are reliable proxies of the whole soft bottom benthic assemblage

in assessing the effects of offshore gas platforms in the Mediterranean. Patterns of variation in polychaetes, in contrast, were not consistent with the general response of whole assemblages at both the species level and at higher taxonomic levels. Opposing results have been found in studies assessing the effects of offshore oil platforms on soft bottom benthic assemblages in other bio-geographic contexts (Olsgard and Somerfield, 2000). Variation in the related-

Table 3
Spearman's correlation (ρ) values between the species similarity matrix and matrices at higher taxonomic levels calculated for all data sets (untransformed data).

	LB	SB	OF	HB
<i>Molluscs</i>				
S vs. G	0.989**	0.935**	0.985***	0.974***
S vs. F	0.978**	0.914**	0.941***	0.953***
S vs. O	0.933**	0.693**	0.808***	0.851***
S vs. C	0.811**	0.382**	0.679***	0.716***
<i>Polychaetes</i>				
S vs. G	0.911**	0.967**	0.929***	0.799***
S vs. F	0.750**	0.908**	0.841***	0.631***
S vs. O	0.618**	0.842**	0.746***	0.433***

S: species; G: genus; F: family; O: order; C: class.

** $P < 0.01$.

*** $P < 0.001$.

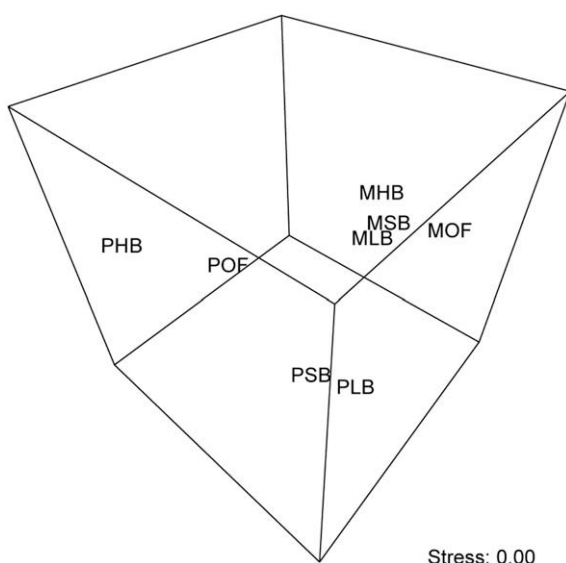


Fig. 3. Third-stage MDS ordination 3-d plot based on second-stage similarity matrices of all data sets. M = molluscs, P = polychaetes. LB = LB offshore platform, OF = sewage outfall, HB = hard bottom natural gradient, SB = soft bottom natural gradient.

ness of species within higher taxa and/or shifts in dominance amongst groups of organisms within assemblages occurring in different bio-geographic regions could affect the effectiveness of taxonomic surrogates (e.g., Roy et al., 1996; Price et al., 2006). The most abundant and diverse group of organisms is likely the best for depicting the response of the whole assemblage, even at a low taxonomic resolution, especially if higher taxa generally only include one species or a small number of species (Musco et al., 2009). This could be the case in the Mediterranean offshore platform study site, where molluscs represented the dominant component of the whole assemblage (see Table 1). The performance of taxonomic surrogates could also be affected by the nature of the impact, as the degree of tolerance or sensitivity to a given environmental stress can vary among different groups of organisms (Pearson and Rosenberg, 1978; Gray and Pearson, 1982). In other words, at low taxonomic resolution, environmental stressors affecting selected taxa (e.g., particular families) are more likely to be detected than other stressors that unselectively influence all species within a given group of organisms. The impact of the investigated offshore platform seemed to be mostly related to alterations of substrate heterogeneity than to pollution (Terlizzi et al., 2008). Most polychaete species are susceptible to change in substrate features (Schatzberger et al., 2008), whereas in molluscs, the sensitivity or

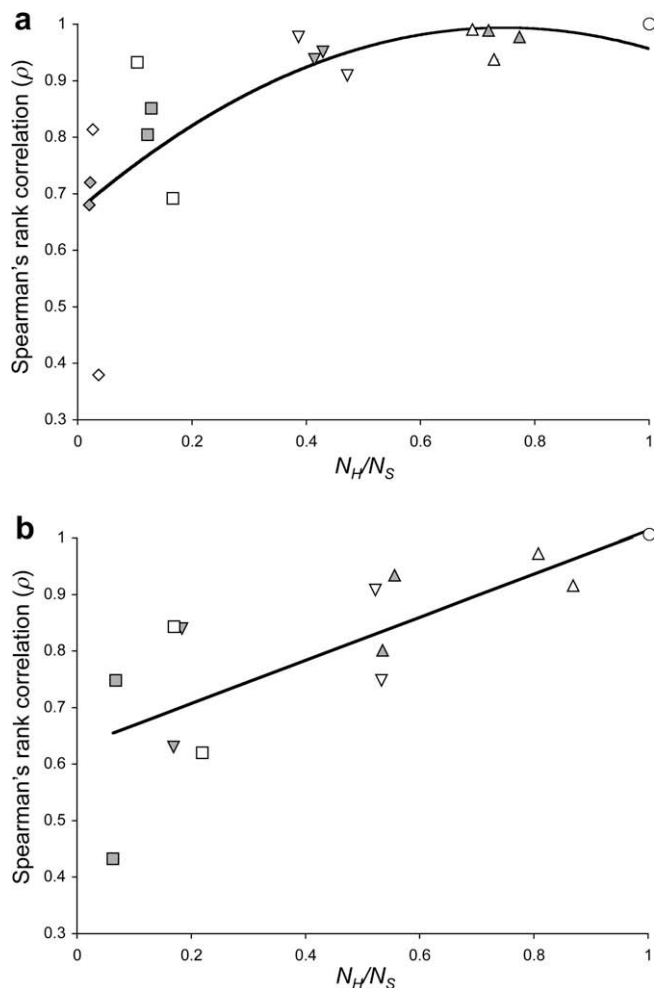


Fig. 4. Scatter plots of Spearman's rank correlation values (ρ) against the N_H/N_S ratios (see text for details) for (a) molluscs and (b) polychaetes. \circ = Species, \triangle = Genus, ∇ = Family, \square = Order, \diamond = Class (molluscs only). Blank symbols = soft bottoms, grey symbols = hard bottoms.

tolerance to substrate heterogeneity could be shared amongst species within a single genus or family (e.g., Alexander et al., 1993; de la Huz et al., 2002). Polychaete species and their higher taxa, however, demonstrated significant variation at different distances from the platform, but the spatial pattern of variation shown by the whole benthic assemblages and molluscs could not be discerned. Distinct groups of organisms analyzed at a low taxonomic resolution could reflect a given human impact, although with a lower ability to assess the spatial extent of the impact. In this respect, the choice of the sufficient taxonomic level and/or the surrogate represents a crucial step in the assessment of anthropogenic threats, due to the strong implications for related management and mitigation strategies.

In terms of the assessment of human impacts on hard substrates, previous studies revealed a similar significant effect on other ecological groups, such as sessile organisms (Terlizzi et al., 2005b), meiofauna (Fraschetti et al., 2006) and fish assemblages (Guidetti et al., 2003). The present study suggested that polychaete and mollusk families, and even orders, could be used as efficient taxonomic surrogates in detecting the effects of sewage discharge on a subtidal rocky reef in the Mediterranean, and are proposed to be promising indicators of an ecosystems' response to sewage pollution in a temperate rocky subtidal zone. Molluscs, in particular, could respond efficiently to taxonomic aggregation in detecting the impact of sewage discharge in temperate rocky reefs (Smith

and Simpson, 1993). In such habitats, most mollusk families are generally mono-specific or included very few species (Terlizzi et al., 2003b, 2005a). Moreover, in the few speciose families (e.g., Rissoiidae), sewage discharge mostly affected a single species by drastically increasing its abundance (Terlizzi et al., 2005a). Polychaetes were able to discriminate between the sewage location and unpolluted controls even at a low taxonomic resolution, though it has been hypothesized that the generally low N_H/N_S ratio of polychaete assemblages inhabiting hard substrates could limit their utility in TS-based approaches in such habitats (Giangrande et al., 2005). The low N_H/N_S ratio characterizing hard substrate polychaetes is mostly determined by a few very speciose families (e.g., Syllidae), whereas the remaining families comprise one or few species, some of which are very abundant and are strongly affected by the sewage impact. Thus, the use of TS in groups of organisms that appear to be less prone to taxonomic surrogacy due to their taxonomic structure, can lead to appreciable results if the impact mostly affects dominant and taxonomically unrelated species (Musco et al., 2009).

As found elsewhere (Olsgard et al., 1998; Lasiak, 2003; Włodarska-Kowalczyk and Kędra, 2007), this study showed that transforming data could influence the results of analyses as well as taxonomic aggregation. The effects of transformations varied across habitats and environmental conditions, depending on the inconsistencies in ecological responses of assemblages to different sources of environmental change. In hard bottoms, sewage discharge and variation in depth mostly affected the abundance of taxa (Smith and Simpson, 1993; Olabarria and Chapman, 2001). In soft bottoms, the impact of platform and depth gradients are typically related to changes in environmental variables, such as sediment grain, which could affect both the abundance and identity of taxa (Bomkamp et al., 2004; Giangrande et al., 2005). In contrast to predictions by Clarke and Warwick (1994), such findings suggest that no transformation, and even mild transformations, can provide a 'best view' of the structure of assemblages. In the absence of previous acknowledgements, untransformed data should be analyzed, since it is often difficult to recognize *a priori* how environmental variation will affect the structure of assemblages (e.g., influencing rare or abundant taxa). Data transformations could derive useful information to determine an accurate approximation for assessing the abundance of taxa able, which could facilitate sample processing (Olsgard et al., 1998).

TS is thought to be able to detect human impacts but not variation in assemblages along natural gradients in environmental variables (e.g., water depth, sediment granulometry). Unlike human impacts, natural environmental gradients are thought to drive the replacement of closely related species rather than causing shifts at higher taxonomic levels (Warwick, 1988a), although the results of recent studies have put this assumption under debate (e.g., De Biasi et al., 2003). It should be noted, however, that most of these studies focused on all taxonomic groups combined, testing the TS efficacy in relation to strong natural disturbances (e.g., Włodarska-Kowalczyk and Kędra, 2007) or large geographical gradients (e.g., Dethier and Schoch, 2006). Differences at the regional scale or larger scales in higher taxa are commonly observed in marine invertebrates (Price et al., 1999; Anderson et al., 2005; Bevilacqua et al., 2009). Strong disturbances, even from natural disturbances, could produce variation in assemblages that are as pronounced as those produced by human impacts (e.g., Dolbeth et al., 2007). Our results from natural environmental gradients in different habitats and taxonomic groups illustrated a more complex scenario. Independently of the type of organisms or habitat considered, differences in assemblages were detectable up to a higher taxonomic level in impacted conditions compared to natural conditions. In natural environmental gradients, however, patterns of variation in assemblages were always retained to at least

the family level for mollusks, whereas for polychaetes, patterns of variation in assemblages were not observed after the genus level. In study cases of impacts, a long history of anthropogenic perturbation could have led to a 'hierarchical response to stress' in benthic assemblages (Pearson and Rosenberg, 1978; Boesch and Rosenberg, 1981; Ferraro and Cole, 1990). Moreover, the magnitude of the effects of human impacts (i.e., offshore platform and sewage outfall) was probably higher than that of natural gradients and, therefore, was less susceptible to being smoothed out when species were aggregated into higher taxa. Such mechanisms could be the reason for the more efficient response of higher taxa in impact cases, but did not explain why the same natural gradients produced patterns of variation in mollusks that were more robust to taxonomic aggregation at the family level than in polychaetes. Such inconsistencies were clearly not due to discrepancies in environmental and/or experimental contexts, as the type of natural gradients and experimental procedures were exactly the same for both groups of organisms. Also, variation in the taxonomic relatedness of species amongst families did not fully explain the different responses between mollusks and polychaetes. The proportion of mono-specific families was comparable between the two groups (Terlizzi et al., 2005a, 2008; Giangrande et al., 2003) and, though mollusk families showed higher N_H/N_S ratios in both of the habitats studied than in hard substrate polychaetes, polychaete families in soft bottoms exhibited the highest values but did not perform better than hard substrate polychaetes.

Patterns of decreasing N_H/N_S ratios with increases in the taxonomic level and the corresponding decline in rank correlations between species-level matrices and matrices of higher taxa overlapped tightly among mollusk data sets up to the family level. This implies that, in mollusks, mechanisms behind TS could act homogeneously across habitats and environmental conditions. In contrast, for polychaetes, such patterns were largely inconsistent among study cases, indicating that multiple factors could interact to determine their robustness to taxonomic aggregation. Different groups respond differently to environmental variation, but the response can be related to the taxonomic level only if species respond more or less uniformly within higher taxa. As stated by Warwick (1993), families generally represent fairly homogeneous groups of organisms sharing basic functional traits. However, the level of such intra-family functional redundancy could depend on the classification criteria adopted and on taxonomic traditions (Bertrand et al., 2006), which may be not consistent across phyla (Warwick and Somerfield, 2008). In mollusks, structural traits identifying families (e.g., feeding habits, life cycles) are likely to be strongly linked to functional properties of the organisms included (Terlizzi et al., 2009). In polychaetes, such relationships appear to be less clear since, in contrast to the morphological homogeneity, some of the most speciose polychaete families are characterized by a high plasticity of feeding habits (Fauchald and Jumars, 1979; Giangrande et al., 2000). Our findings support this assumption, suggesting that, unlike with polychaetes, mollusk families could represent an effective surrogate of species independent of the environmental context.

The potential to reduce the costs and the time associated with taxonomic identification represents an appreciable property of TS that is appealing when rapid impact assessments (Dauvin et al., 2003; Gomez Gesteira et al., 2003) or continuous monitoring are required (Olsgard et al., 1997, 1998). However, the taxonomic units that should be targeted in marine environmental studies are unlikely to be univocally agreed upon. The consequent proliferation of TS studies has led to a fragmented knowledge, with the hidden risk of causing people to renounce taxonomy (Maurer, 2000; Terlizzi et al., 2003a; Giangrande, 2003). Not all marine ecologists are, or have easy access to, expert taxonomists. This is a crucial issue, perhaps even more important than the issue of cost, in sustaining the

interest around TS in marine systems. Currently, factors influencing the effectiveness of TS still require a great deal of clarification (Dethier and Schoch, 2006) since most attempts have been focused on finding the general taxonomically sufficient level, rather than on building a general theory on TS. Further efforts aimed at understanding ecological and biological reasons underlying the agreement in the responses of species and higher taxonomic ranks are strongly needed to provide a general framework for the application of TS in marine systems.

Acknowledgements

C. Vaglio and G. Guarnieri provided invaluable assistance during fieldwork. D. Scuderi, D. Fiorentino, A.L. Delos and S. Felling assisted with the sample processing and sorting and with species identification. Thanks to J. Claudet for valuable comments on regression analyses. Financial support was provided by Eni S.p.A., PEET (Partnerships for Enhancing Expertise in Taxonomy), and MURST (COFIN and FIRB projects). The authors acknowledge the support by the MARBEF Network of Excellence “Marine Biodiversity and Ecosystem Functioning”, which is funded in the Community's Sixth Framework Programme (contract no. GOCE-CT-2003-505446) and the E.U. Integrated Project SESAME.

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