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The use of coarser taxonomic resolution in studies of predation on marine sedimentary fauna

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Abstract

Given the logistical difficulties, cost, and time involved in species-level identifications, several authors have proposed the use of coarser taxonomic resolution (e.g. family, order) in studies of pollution. The use of surrogates instead of species relies on their sufficiency to detect community responses to the pollution gradient without appreciable loss of information. No studies, however, have applied this approach to experimental studies such as community responses to predation disturbance and evaluated the performance of surrogates at the spatial scales typical of experiments. We addressed both problems by analyzing the results of three predation experiments carried out in Bonne Bay, Newfoundland. We pooled species data into coarser taxonomic categories (family to class) and determined whether effects of predation that were evident at the species level were also evident with the use of each coarser surrogate and increasing data transformation. Our results indicate that non-transformed data at the family level represent a reasonable surrogate of species; however, the ability to discriminate between ambient and (predator) manipulated sediments is gradually lost with data transformation and with the pooling of species into coarser taxonomic categories. Successive data transformation indicates that in this system predation plays a strong role on dominant but not necessarily rare species. Moreover, our results suggest that varying reliability of surrogates precludes the identification of a single general level of taxonomic sufficiency to be used in experimental studies. The use of surrogates, therefore, is suggested only after scrutiny and evaluation, and should be limited to preliminary studies where biodiversity has been well described.
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1. Introduction

The last decade has seen renewed interest in marine biodiversity and concern for our inability to identify large numbers of marine invertebrates (Snelgrove, 1999; Gray, 2001). Most of this problem derives from the time, skills, and resources required for identification, particularly at the species level (Ferraro and Cole, 1995). The lack of taxonomic expertise and the worldwide growth of research and exploration are the two main components of what Giangrande (2000) called a "taxonomic impediment". Several surrogates of species have been proposed in order to circumvent this problem. Proposals include indicator groups such as some highly diversified

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polychaetes (Olsgard et al., 2003), indicator ratios such as "nematodes/copepods" for meiobenthos (Amjad and Gray, 1983) or "polychaetes/amphipods" for macrobenthos (Gomez Gesteira and Dauvin, 2000), and subsampling of pre-defined numbers of specimens (King and Richardson, 2002). Each of these approaches has proven useful in some applications but has failed to accurately predict patterns of biodiversity elsewhere. A fourth approach is the use of coarser taxonomic categories such as genera, families, etc. (Somerfield et al., 1995). The feasibility of using coarser taxonomic levels has been studied in freshwater habitats (Bowman and Bailey, 1997), rocky shores (Pagola-Carte and Saiz-Salinas, 2001), gravel and sandy beaches (Schoch and Dethier, 2001; Defeo and Lercari, 2004), lagoons (Mistri and Rossi, 2001), and coastal (e.g. Somerfield and Clarke, 1995; Gray et al., 1988, James et al., 1995) and deep-sea sedimentary communities (Narayanaswasny et al., 2003).

The use of coarser taxonomic resolution relies on the idea of "taxonomic sufficiency" (hereafter TS) formally introduced by Ellis (1985). This approach justifies the use of coarser taxonomic categories instead of species, when loss of information has no significant effect on the comparison of communities in question (e.g. a pollution gradient, Warwick et al., 1988; Gray et al., 1988; Olsgard et al., 1997). Broader taxonomic categories appear not only to "suffice" in detecting pollution gradients but also to remove some degree of redundancy attributed to the use of species and that arguably may mask pollution effects (Warwick, 1988, 1993; Gray et al., 1988). Moreover, coarser taxonomic resolution is less affected by the lack of taxonomic consistency frequently detected in species-level comparisons, and that otherwise would preclude the proper comparison of surveys (Olsgard et al., 2003). Despite these arguments and its increasing popularity, TS remains controversial (May, 1990; Maurer, 2000). More studies are therefore required to verify the applicability of TS in studies of natural as well as anthropogenic-related sources of variation.

Three observations suggest that further exploration of TS in studies of natural variation is necessary and relevant. First, anthropogenic gradients (e.g. oil fields or sewage dumps) likely represent more intense forms of perturbation than natural gradients, and therefore, community responses and surrogate performance are expected to be different (cf. Vanderklift et al., 1996; Olsgard et al., 1998). The intensity of these perturbations would also change depending on the relative influence of predators on a few dominant species or a more extended set of rare species (Lasiak, 2003). Second, the spatial scale of patterns typically studied with surrogates (oil fields, monitoring surveys) is far larger than the typical scales of studies and experiments on natural variation (Kemp et al., 2001). Studies on predation, for example, may account for differences in benthic community structure (Ólafsson et al., 1994) that are far more localized and less severe than the changes expected from pollution. Like other sources of natural variation in benthic communities, predation often induces species replacement and changes in density rather than in number of species.

A third observation is methodological. Traditional analyses that compare results obtained with different taxonomic levels often rely on visual comparisons of sample similarities (e.g., non-metric multidimensional scaling plots or nMDS). A much-needed aspect in studies on adequate taxonomical resolution is therefore the application of quantitative criteria (Vanderklift et al., 1996). Three of these criteria are used here to analyze the feasibility of using surrogates in experimental predation studies on soft-sediments communities: i) Second-Stage correlation (a PRIMER nMDS routine that allows comparison of different taxonomic levels) between similarity matrices resulting from data aggregated at taxonomic levels from species to class; ii) MDS stress and similarity of treatments in cluster analyses; and iii) Analysis of Similarity (ANOSIM) between control treatments and manipulated communities to evaluate discriminating ability at different levels of taxonomic resolution. In order to examine this question, we used data from three field experiments (two predator exclusions, one predator inclusion) conducted in sedimentary habitats in Bonne Bay, Newfoundland. Previous analyses of the three experiments have already shown the existence of significant predation effects on a number of community response variables (Quijón and Snelgrove, 2005a, and unpublished data). Thus, the three data sets can be used to evaluate the TS performance for experimental studies at relatively small spatial scales.

2. Materials and methods

2.1. Field experiments

Two exclusion experiments were conducted in each of the two arms (South and East Arms) of Bonne Bay, Newfoundland, and described in detail by Quijón and Snelgrove (2005a). Briefly, the experiments consisted of full (exclusion) and partial cages (potential artifact effects) deployed in sedimentary habitats at ~30 m

deep. Fauna from the cage treatments was compared with ambient sediments by collecting replicate samples (7-cm diameter cores, 2 cores per sample, 0–10 cm deep) to monitor for changes after 4 and 8 weeks of predator exclusion. An additional experiment was carried out in East Arm and involved the inclusion of snow crabs (*Chionoecetes opilio*; an abundant epifaunal predator in the bay) in full cages (one individual per cage) similar to those used in the exclusion experiments. Snow crabs were confined in cages for 4 days, after which time faunal samples similar to those described above were collected from cages and ambient sediments.

Original statistical analyses of both exclusion experiments as well as the inclusion experiment (Quijón and Snelgrove, 2005a) were conducted with univariate (ANOVA) and multivariate methods (clustering and Principal Component Analysis of Chord Normalized Expected Species Shared, CNESS). All of the above analyses were carried out with non-transformed data of organisms identified at the species level. Overall, these analyses indicated i) the lack of caging artifact effects on sedimentary or faunal variables and ii) the existence of significant effects of predation on species composition, abundance and, in some cases, the diversity of the communities. The effects detected in the (snow crab) inclusion experiments were consistent with the results obtained in the exclusion experiments and with additional laboratory experiments carried out with two different densities of the two most important predators in the bay: snow crab and rock crab (*Cancer irroratus*; Quijón and Snelgrove, 2005b).

2.2. Analysis of taxonomic resolution

In order to test whether the differences between ambient and manipulated (exclusion or inclusion of predators) treatments that were detected at the species level were also observed at coarser taxonomic resolution, the three sets of data were analyzed using PRIMER routines (Clarke and Warwick, 1994). Because no artifact effects were detected in the original exclusion experimental analyses and in subsequent re-analyses using PRIMER, only control and manipulated (exclusion or inclusion) treatments after 4 and 8 weeks of experimentation were used in the procedures described below. This reduced the pool of species from 78 to 50–51 per site (Table 1).

First, data at the species level were successively aggregated into family, order, and class levels (cf. Table 1). Data at the genus level were not considered because their outcomes were virtually identical to species data; genera with more than one species were restricted to only a few cases (3 taxa), which were all relatively low in abundance. Bray–Curtis similarity matrices using raw and transformed data were then created for each level of taxonomic resolution. Data transformation included square root (hereafter √), fourth root (√√), and presence–absence (+/−). The purpose of these transformations was to diminish the relative importance of numerically dominant species (expressed in the raw data) to emphasize community-wide attributes and rare species (√, √√) to the point where every species was weighted equally (+/−) (Olsgard et al., 1997).

Table 1
Number of sampling units (replicates × treatments × sampling periods) and taxonomic units at each level of taxonomic resolution

	Exclusion South Arm	Exclusion East Arm	Inclusion East Arm
# Sampling units	4 × 2 × 2 = 16	4 × 2 × 2 = 16	4 × 2 × 1 = 8
# Taxonomic units			
– Species	50	51	39
– Family	39	40	33
– Order	20	18	13
– Class	6	5	5

Next, the sixteen similarity matrices generated for each original data set were compared with rank correlations using the Second-Stage routine of PRIMER. High similarity values (close to 100) suggest a high degree of correspondence between pairs of similar matrices and therefore no overall changes between data analyzed at different taxonomic levels. We used Second-Stage instead of RELATE to avoid/minimize independency constraints. The similarity matrices were also used to generate multidimensional scaling (MDS) plots to represent the relatedness of samples and treatments in a two-dimensional space. Stress values associated with each MDS plot reflect how well the distance among samples in the plot represent the actual distance among samples (Clarke and Warwick, 1994) and were also used to compare between taxonomic levels. Group Average cluster analysis was subsequently applied to Bray–Curtis dissimilarities of the groups visualized in the MDS plots. In particular, we focused on the level of similarity at which the groups of samples from controls and manipulated sediments were linked together. Although this level of similarity is arbitrary, it is useful in visualizing at what level treatments become indistinguishable.

Finally, control and manipulated sediments were compared with Analysis of Similarity (ANOSIM). This test compares groups of samples defined a priori in a

Table 2
Rank correlations (degree of correspondence between pairs of similarity matrices) from Second-Stage analyses obtained at different taxonomic resolutions

Experiment	Level	Raw			√			√√			+/−		
		Spp	Fam	Ord	Spp	Fam	Ord	Spp	Fam	Ord	Spp	Fam	Ord
Exclusion South Arm	Spp	–			–			–			–		
	Fam	96.9	–		94.4	–		91.8	–		89.4	–	
	Ord	91.5	93.7	–	87.2	90.6	–	78.6	82.8	–	70.6	74.8	–
	Cla	73.1	74.6	78.5	59.6	63.3	70.6	50.6	54.1	65.5	51.8	55.9	67.1
Exclusion East Arm	Spp	–			–			–			–		
	Fam	97.3	–		95.5	–		94.3	–		94.0	–	
	Ord	91.3	91.9	–	87.8	89.9	–	82.9	85.6	–	77.6	79.8	–
	Cla	81.5	81.5	92.9	72.6	73.2	84.2	61.9	60.4	69.2	54.0	50.4	60.9
Inclusion East Arm	Spp	–			–			–			–		
	Fam	97.6	–		95.3	–		94.5	–		94.0	–	
	Ord	88.7	88.3	–	82.7	82.2	–	78.1	76.6	–	74.7	72.8	–
	Cla	65.0	63.9	75.2	49.7	49.5	68.1	36.7	40.6	56.8	30.7	33.2	46.6

Analyses were carried out with raw and transformed (√, √√, +/−) data. Spp = species, Fam = family, Ord = order, Cla = class.

similar way as an ANOVA analysis, weighting variation within versus between groups (treatments). The ANOSIM routine generates an *R*-statistic (−1 to +1) and a significance test. High *R*-statistic values indicate that ANOSIM is able to discriminate between treatments at a particular taxonomic level. Because exclusion experiment data include two independent comparisons (after 4 and 8 weeks of predator exclusion), they were treated separately (cf. Table 3).

3. Results

3.1. Similarity matrices

Pair-wise comparisons of similarity matrices for each set of data are summarized in Table 2. Rank correlations were always highest for the comparison of species–family matrices (0.89–0.98), particularly when using non-transformed data (>0.96). Species–

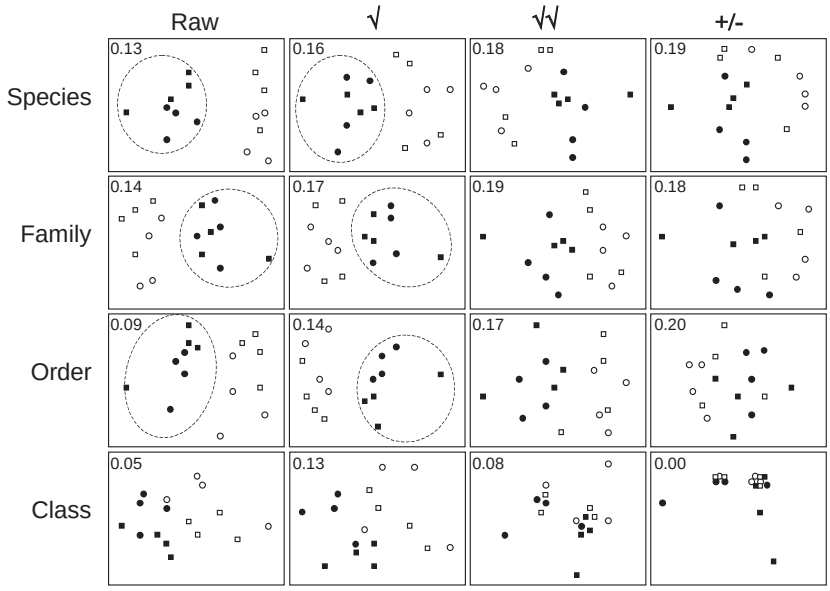

Fig. 1. MDS plots of control (open symbols) and predator exclusion (filled symbols) treatments in the South Arm Experiment. Predation effects are compared after 4 (circles) and 8 (squares) weeks of exclusion, using four taxonomic resolutions, and raw and transformed data. Numbers are stress values. Dotted lines encircling exclusion treatments have been plotted in those analyses were clusters of Bray–Curtis similarity distinguished treatments as two individual branches (see text).

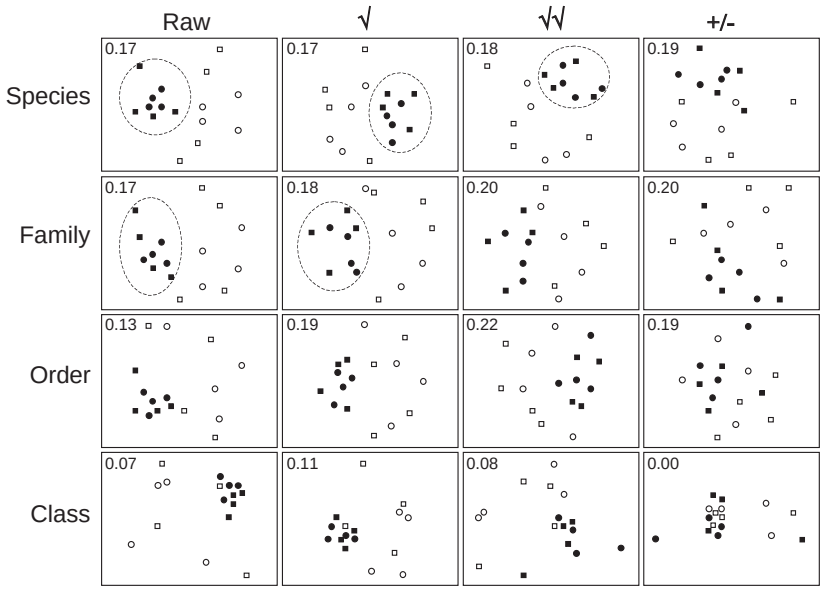

Fig. 2. MDS plots of control (open symbols) and predator exclusion (filled symbols) treatments in the East Arm Experiment. Other details as in Fig. 1.

family correlations decreased with severity of data transformation (raw to +/−) but were consistently higher than any other corresponding (at the same level of transformation) pair-wise correlation between taxonomic levels. Correlation values also decreased with the successive comparison between taxonomic levels (family–order, order–class) (Table 2).

3.2. MDS and cluster analyses

Groups of samples from ambient (open symbols) and manipulated (filled symbols) communities were clearly separated when species-level data were plotted in two-dimensional space (Figs. 1, 2, and 3). However, treatments become increasingly similar (and intermixed)

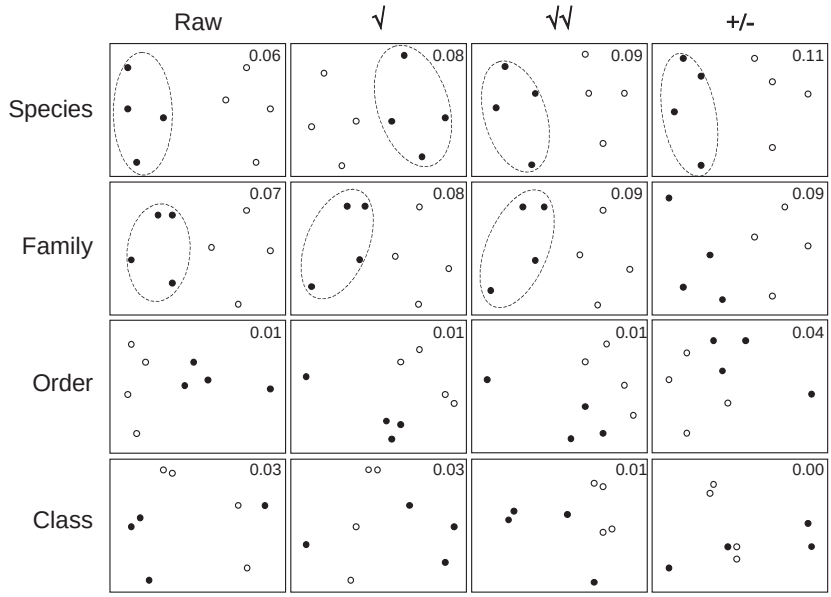

Fig. 3. MDS plots of control (open symbols) and predator inclusion (filled symbols) treatments in the (snow crab inclusion) experiment in East Arm. Other details as in Fig. 1.

with the aggregation of data to coarser taxonomic categories (family to class) and with more severe data transformation. In both exclusion experiments (Figs. 1 and 2), the stress values generally increased from species to order (0.09–0.20), but then decreased at the class level (0–0.13). In the inclusion experiment, the stress increased from species to family (0.06–0.11) and decreased in order and class (0.00–0.04).

Some cluster analyses separated control from manipulated communities as two simple branches (dotted lines in Figs. 1–3), making the distinction between treatments straightforward. However, these cases were restricted to species- and family-level analyses for East Arm experiments, and to species through order levels in South Arm. The comparison of Bray–Curtis similarities of control and manipulated groups of samples is presented in Table 3 and Fig. 4. For the three sets of data, Bray–Curtis similarity values consistently increased 30–40% with the aggregation of species in coarser taxonomic categories (rows of Table 3) but rate of change was small between species and family relative to coarser taxonomic levels (Fig. 4). The transformation of data also contributed to increased similarity between treatments, but this increase was ~10% (compare columns of Table 3).

3.3. Analysis of similarity

The ability to discriminate between treatments (indicated by a significant *R*-statistic value) was evaluated with ANOSIM (Table 4). In general, with the aggregation of data at coarser taxonomic levels, the *R*-statistic values decreased and the number of contrasts with no significant differences ($P>0.05$) increased. The ability to discriminate between controls and predator manipulation treatments (exclusions or inclusions) was greatest at the species level (16 of 20 comparisons) and was almost completely lost at the class level (significant differences in only 7 of 20 comparisons). Family- and order-level comparisons produced somewhat similar findings (14 out of 20 significant differences) to species-level comparisons but the *R*-values were generally higher at the family level. As in the earlier analyses, increased severity of data transformation was more frequently associated with non-significant differences between treatments (reduced discriminatory ability; Table 4).

Table 3
Bray–Curtis similarity values linking controls and manipulated (exclusion or exclusion of predators) treatments in Group-average cluster analyses

Experiment	Transformation	Species	Family	Order	Class
Exclusion South Arm	Raw	42.54	46.59	57.48	71.69
	√	51.00	47.60	69.07	84.10
	√√	50.83	51.04	73.15	82.98
	+/−	54.53	54.07	74.76	80.44
Exclusion East Arm	Raw	35.82	39.37	51.98	61.49
	√	41.38	46.55	63.47	75.23
	√√	42.18	49.62	69.00	82.99
	+/−	42.82	52.26	74.58	84.82
Inclusion East Arm	Raw	30.52	34.05	43.57	62.84
	√	35.81	39.90	54.99	72.60
	√√	38.20	38.97	60.97	73.51
	+/−	40.37	40.85	66.86	73.33

Data from different taxonomic resolutions using raw and transformed (√, √√, +/−) data.

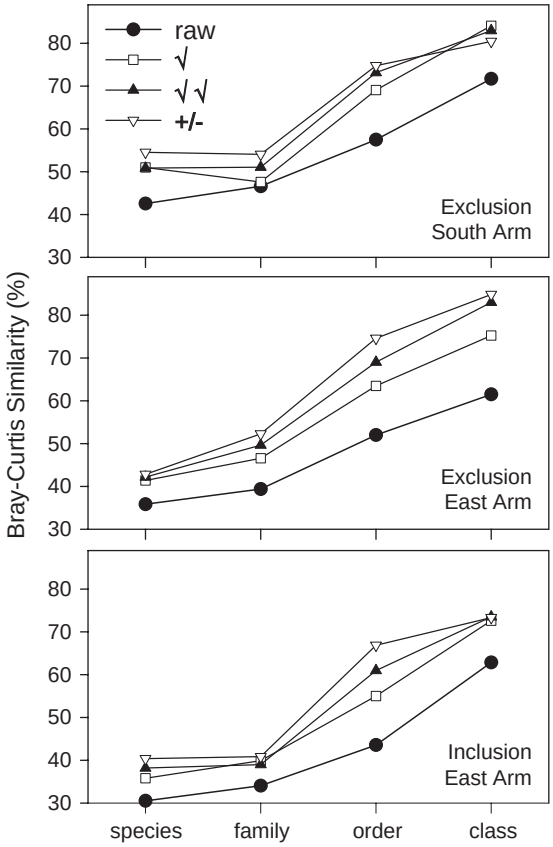

Fig. 4. Variation in Bray–Curtis similarity linking controls and manipulated (exclusion/inclusion) treatments for different levels of taxonomic resolution (species–class) in the three sets of experimental data. Results from raw and transformed data are plotted.

4. Discussion

Few studies have applied TS in the analysis of factors that generate natural rather than anthropogenic variation in benthic community structure (Dauvin et al., 2003). This situation is likely related to the lower

Table 4
Values of the *R*-statistic from one-way ANOSIM comparing between ambient (control) and manipulated (predator exclusion or inclusion) communities, at different taxonomic resolutions

Experiment	Time	Transformation	Species	Family	Order	Class
Exclusion South Arm	4 weeks	Raw	0.95*	0.93*	0.65*	0.39*
		√	0.85*	0.92*	0.87*	0.32NS
		√√	0.65*	0.74*	0.88*	0.22NS
		+/−	0.36NS	0.50NS	0.73*	0.06NS
	8 weeks	Raw	0.83*	0.83*	0.67*	0.67*
		√	0.41*	0.41NS	0.60*	0.55*
		√√	0.23NS	0.20NS	0.49*	0.29*
		+/−	0.13NS	0.04NS	0.32NS	0.12NS
Exclusion East Arm	4 weeks	Raw	0.77*	0.73*	0.67*	0.64*
		√	0.69*	0.65*	0.66*	0.73*
		√√	0.63*	0.50*	0.38NS	0.51*
		+/−	0.54*	0.44*	−0.14NS	0.12NS
	8 weeks	Raw	0.40*	0.52*	0.30*	0.21NS
		√	0.44*	0.45*	0.38*	0.30NS
		√√	0.40*	0.29NS	0.23NS	0.18NS
		+/−	0.25NS	0.23NS	0.12NS	−0.13NS
Inclusion East Arm		Raw	0.92*	0.73*	0.55*	0.06NS
		√	0.88*	0.65*	0.51*	0.32NS
		√√	0.82*	0.59*	0.41*	0.35NS
		+/−	0.74*	0.60*	0.26NS	0.30NS

For the exclusion experiments, comparisons were done separately for predation effects after 4 and 8 weeks. Asterisks (*) and "NS" indicate significant and non-significant differences, respectively.

performance that TS is expected to play in less polluted areas, as recently shown for Norwegian benthos (Olsgard and Somerfield, 2000). Our results include three lines of evidence to suggest that the use of surrogates may be adequate in order to detect differences in experimental studies such as those looking at predation effects (see below). However, our results also suggest that not just any taxonomic resolution will suffice.

4.1. Correlation of similarity matrices

Second-stage species–family rank correlations using non-transformed data were the highest among all possible pair-wise comparisons in the three data sets. This result is particularly important given that correlation of similarity matrices is the most powerful tool to evaluate TS performance (Somerfield et al., 2002). Levels of similarity in species–family correlations after data transformation gradually decreased, although they remained clearly higher than any other correlation between species and order or species and class levels. Although these analyses do not discriminate significant from non-significant correlations, their results suggest limitations for the use of surrogates other than genus or family, as already shown in studies on macrobenthos (James et al., 1995) and meiobenthos (Gray et al., 1988).

4.2. MDS and cluster analyses

MDS plots do not offer an objective criterion for separating good from poor taxonomic resolution (Vanderklift et al., 1996). However, they help to visualize gradual changes in sample similarity and the smothering effect of coarser resolution and data transformation (Olsgard et al., 1997). This is relevant in studies of natural variation (e.g. Schoch and Dethier, 2001) where community responses are generally weaker than in pollution studies (Olsgard et al., 1998; Karakassis et al., 2002). In predation studies, for instance, "strong" effects result in changes ≥100% of prey density (Ólafsson et al., 1994). This is not the norm in sedimentary communities, and in fact does not represent the more modest predation effects detected in Bonne Bay (Quijón and Snelgrove, 2005a,b). In this area, exclusion of predators significantly increased total densities (up to ~57% on average) but not the number of species (up to ~30%). Cluster analyses separated controls and manipulated treatments as individual branches in only a few cases, confined mostly to raw and weakly transformed data at the species or family levels. Coarser resolution (order and class) increasingly inter-mixed different treatments, suggesting limitations for their use as surrogates of species.

Stress values increased from species to family or order, and then decreased in the class level. A similar pattern of variation was reported in a pollution study (Vanderklift et

al., 1996), although previous studies have also found a simple decrease or no major changes in stress (e.g. Somerfield and Clarke, 1995). Variation of stress estimates with increasing taxonomic resolution may be related to the reduction in the "# taxa/# samples" ratio, and with the increase in non-zero values in the data (Vanderklift et al., 1996). Although the biological significance of both ratios is not straightforward, the lower stress values detected at the class level simply suggest that these MDS plots are better representations of the actual distances among samples (Clarke and Warwick, 1994). For the purposes of this study, however, it does not imply that class is a better surrogate of species than family or order.

4.3. Analysis of similarities

The ability of ANOSIM to discriminate between treatments decreased with coarser taxonomic resolution and with increasingly strong data transformation. When aggregated at coarser taxonomic levels, species response to stress may undergo compensatory changes that reduce the sensitivity of some surrogates (Frost et al., 1992). This appears to be the case at the class level, where ANOSIM frequently failed to discriminate between treatments ($P>0.05$). Although not presented here, a similar inability to discriminate between treatments is observed with further taxonomic aggregation (e.g., phylum). Previous studies have found that in some intertidal habitats, class or even phyla are useful surrogates of species (Krassulya, 2001; Defeo and Lercari, 2004). However, the disturbances in those studies were strong and persistent enough that they would likely be reflected at almost any taxonomic resolution (Olsgard et al., 1998; Warwick, 1988). The ANOSIM R-statistic is also a useful tool to evaluate discriminating ability (Clarke and Warwick, 1994). As expected, R-statistic values decreased with species aggregation (Warwick, 1988) and data transformation (Bowman and Bailey, 1997; Somerfield and Gage, 2000). Correlation coefficients were calculated to visualize how closely surrogates resemble species in terms of R-statistic values (see Table 4); correlations coefficients declined from 0.91 (species–family) to 0.41 (species–order) and 0.43 (species–class). Although the rigour of these comparisons may be argued, it is clear from this and previous analyses that data at the family level resembles species data considerably better than order and class.

4.4. Natural variation and the use surrogates

Several studies have suggested that family is a good surrogate of species (Somerfield and Clarke, 1995; Dauvin et al., 2003), and the best compromise between accuracy and cost-effective processing (Ferraro and Cole, 1995). For Bonne Bay, the use of family as an acceptable surrogate of species relies on two aspects of our data. First, it is the result of low number of species per family (cf. Table 1). This attribute reduced the chances of comparing families with very different number of species, a problem that constrains the use of TS in spatial comparisons (May, 1990; Prance, 1994). Second, the effects of predation included the aggregation and quick dominance of a few species in predator exclusion treatments (e.g. the polychaete *Phöloe tecta*; Quijón and Snelgrove, 2005a). This change resembles the local effects of a pollution gradient, where few tolerant/opportunistic species become dominant (e.g. Pearson and Rosenberg, 1978). Increasing data transformation made these results even more evident, given that species-level and virtually all coarser levels gradually lost their capacity to discriminate predator and control treatments. None of these aspects are peculiar to our experiments (cf. Lasiak, 2003), but they suggest restricting the use of surrogates such as families to systems where predation induces strong changes in dominance among prey species.

The justification for the use of surrogates of species is largely practical, and includes limitations in time, skills, cost, and expertise (Ferraro and Cole, 1995). However, there are additional unexplored reasons that, in the case of predation experiments, involve a different type of question: do predators alter community structure by changing the balance among higher (coarser) level taxa? We do not intend to address this question here but the reanalyses of available data sets based on species-level identification is feasible and would be a relevant contribution to benthic ecology.

The acceptable level of taxonomic resolution is a function of the (anthropogenic or natural) disturbance gradient to which communities are responding (Rakocinski et al., 1997). Indeed, some studies have found that family-level data do not perform well as species surrogates (Narayanaswasny et al., 2003; Bowman and Bailey, 1997). Therefore, this study does not constitute a call for a generalized use of family-level taxonomy (or any other surrogate) instead of species. Identification to the species level must be achieved whenever possible (Terlizzi et al., 2003), because it constitutes the most traditional entity to define and study biodiversity (Gray, 2001; Hutchings, 1998) and minimizes risk of missing important changes. This is not a reason to ignore a cautious use of surrogates in studies on natural gradients or experimental ecology, as demonstrated here. But the fact that TS approaches are of varying reliability in

different applications suggests that they will be useful only in well-known systems. In experimental studies, its potential use is well justified if there has been a substantial effort invested in preliminary studies that properly identify surrogates and demonstrate their utility.

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