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Different levels of macroalgal sampling resolution for pollution assessment

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ABSTRACT

The effects of using reduced sampling resolutions to study macroalgal vegetation patterns have not been studied sufficiently. Here, we test the influence of taxonomic resolution level, removal of occasional species, aggregation of species abundances into functional groups and data transformation in the detection of a long-term recovery process by phytobenthic intertidal assemblages. Results indicate that the aggregation of species data into the genus level has very little influence. Likewise, almost any significant information is lost when occasional algae are removed. Analyses at the level of families and orders still clearly detect differences between highly degraded and reference vegetation. By contrast, analyses based on class and functional group abundances capture quite different information. The effect of transformation is similar at the different taxonomic levels. Most surrogate measures properly reflect changes in diversity. It is concluded that genus level is the most appropriate surrogate approach for detecting the recovery process.

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1. Introduction

Increasing human pressure on coastal zones has led scientists, politicians and environmental managers to devote more effort to developing properly designed surveillance networks. Establishing a baseline dataset in order to detect further potential impacts and evaluating spatio-temporal changes in biota associated with a reduction in stress sources are among the most common objectives of monitoring studies. When planning a monitoring programme the objectives must be clear, sampling design must include spatial and temporal replicates at appropriate scales to reflect variability (Underwood, 1993) and the sampling resolution has to be capable of demonstrating changes or differences in community structure (Bates et al., 2007). Monitoring of biological assemblages at species level provides several advantages. It enables species richness to be measured (Vanderklift et al., 1998; Dethier and Schoch, 2006), it allows the detection and monitoring of exotic species (Bates et al., 2007) and it benefits from the bioindicator attributes of certain species (Saiz-Salinas and Urkiaga-Alberdi, 1999; Díez et al., 2009; Juanes et al., 2008). However, the expense of data collection and organism identification at species taxonomic level can hinder the maintenance of long term monitoring programmes or restrict their spatial extent (Bates et al., 2007).

Over the last 20 years 'taxonomic sufficiency' (TS) (Ellis, 1985) has been proposed as a possible solution to save time and cost. It

consists of identifying taxa at higher-than-species taxonomic levels with no significant loss of information in detecting differences in assemblage distribution. This approach also allows more spatial and temporal replication (Bates et al., 2007) and reduces the need for taxonomic expertise (De Biasi et al., 2003). TS has been widely tested in the assessment of soft bottom communities (Warwick, 1988; Ferraro and Cole, 1995; Somerfield and Clarke, 1995; Olsgard et al., 1997: De Biasi et al., 2003: Thompson et al., 2003: Sánchez-Moyano et al., 2006). Numerous studies have concluded that this approach could be useful in reaching objectives, although there is no agreement regarding the choice of an appropriate taxonomic level. When macrofaunal community structure results from a strong pollution gradient the impact might be even more clearly detected if assemblages are analysed at the highest taxonomic level, i.e., phylum (Warwick, 1988; Warwick and Clarke, 1993). However, most TS research on soft bottom communities points to family level as the most suitable compromise between accuracy and processing effort (Somerfield and Clarke, 1995; Olsgard et al., 1997; De Biasi et al., 2003; Gomez-Gesteira et al., 2003; Thompson et al., 2003; Sánchez-Moyano et al., 2006; Tataranni et al., 2009).

Comparatively little attention has been paid to the effects of reducing taxonomic resolution in hard bottom marine communities (Urkiaga-Alberdi et al., 1999; Pagola-Carte et al., 2002; Lasiak, 2003; Anderson et al., 2005b), especially in macroalgal vegetation (Bates et al., 2007; Puente and Juanes, 2008). Hirst (2006) found that the impact of taxonomic aggregation varied for faunal and macroalgal assemblages: while family-level identifications were sufficient to discriminate faunal assemblages to a degree comparable to





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species-level identifications, aggregation of macroalgal data to higher taxonomic levels was substantially less informative. By contrast, other studies have indicated that genus or even family-level taxonomic resolution is sufficient to detect differences in phytobenthic communities (Bates et al., 2007; Puente and Juanes, 2008). More research is needed to test whether the general conclusions obtained from research on soft bottom communities are also applicable to macroalgal assemblages (Puente and Juanes, 2008).

Studies dealing with the applicability of TS indicate that the taxonomic level at which significant information in assemblage patterns begins to be lost depends on several factors, such as the type of gradient (Ferraro and Cole, 1990), the biotic component (Hirst, 2006), the biological attribute considered (Pagola-Carte et al., 2002; Lasiak, 2003) and the habitat targeted (Terlizzi et al., 2003). Because the effectiveness of taxonomic surrogates varies with the circumstances of each study, many researchers (Olsgard and Somerfield, 2000; Terlizzi et al., 2003; Bates et al., 2007) have concluded that before any decision is made regarding a possible sufficient taxonomical level detailed information should be collected at species level.

The effectiveness of data aggregation might be also altered by the choice of data transformation. In those studies that examine assemblage distribution patterns, species abundance data are usually transformed to balance the contribution of rare and dominant taxa to intersample similarities. From raw data to presence/absence data, there is a gradient of possible transformations ($\sqrt{}$, $\sqrt{\sqrt{1000}}$ to establish the level of balancing desired. It has been reported that the effect of data transformation is usually stronger when data are aggregated to higher taxonomic levels, as result of alterations in dominance patterns (Olsgard et al., 1997). This interaction between taxonomic resolution and data transformation might decrease the potential of multivariate tools for perceiving differences in assemblage structure (Terlizzi et al., 2003; Puente and Juanes, 2008). Although the effects of mathematical transformations of data in outcomes of analysis might be as determinant as taxonomic aggregation, this factor has as vet not been studied thoroughly (Olsgard et al., 1998; Anderson et al., 2005a; Puente and Juanes, 2008).

Some attempts have also been made to explore the use of methods based on morphological functional groups of macroalgae in order to reduce sampling effort (Phillips et al., 1997; Konar and Iken, 2009). This approach would greatly reduce the number of entities that require identification, but remarkable discrepancies arise from the conclusions on its utility for perceiving changes in assemblages (Tobin et al., 1998; Bates et al., 2007). Further research is needed to test whether functional groups are a suitable surrogate for reflecting community patterns.

Studies focussed on detecting changes in assemblages exposed to pollution stress usually explore possible diversity alterations since the value of this community measure as an indication of environment health is now widely acknowledged (Bianchi and Morri, 2000). Therefore, the increase in the number of species (Gorostiaga and Díez, 1996; Archambault et al., 2001; Soltan et al., 2001) has been pointed to as a response by marine assemblages to water quality improvements. Several studies (Vanderklift et al., 1996; Doerries and Van Dover, 2003; Włodarska-Kowalczuk and Kedra, 2007) have suggested that diversity patterns, evidenced at species level, can be detected when the level of taxonomic resolution is lowered, although there seems not to be any universally preferred level.

To date most publications on surrogacy have dealt with macrofaunal assemblages. Few studies have examined the utility of taxonomic sufficiency for discriminating between macroalgal communities and even those few have focussed on natural environmental gradients (Hirst, 2006; Bates et al., 2007; Puente and Juanes, 2008; Konar and Iken, 2009). The present study differs in that it explores the influence of sampling resolution on the detection of a recovery process by intertidal vegetation subjected to a progressive decrease in pollution. Four factors were checked as potential sources of variation in the final results: (1) higher taxonomic resolution (genus, family, order and class levels); (2) aggregation of species abundances into functional groups; (3) removal of occasional taxa (cover $\leq 0.5\%$) from the full dataset; and (4) different types of data transformation (none, square root, log (x + 1), presence/absence).

2. Methods

The data used were collected during a monitoring study carried out along a polluted gradient in the Abra de Bilbao bay and adjacent coast (Basque Country, N Spain). For decades this area received huge amounts of non-treated wastewaters, which caused a dramatic deterioration of the benthic communities. The progressive application of a general sewerage plan (promoted by the local water authority Consorcio de Aguas Bilbao-Bizkaia) for the metropolitan area of Bilbao (around one million inhabitants) since 1984 has led to an improvement in water quality and a partial recovery of intertidal phytobenthic assemblages (Díez et al., 2009). Nine surveys were carried out at five sites in summer from 1984 to 2008 (Fig. 1): Arrigunaga (Site 1), Azkorri (Site 2), Meñakoz (Site 3), Matxilando (Site 4) and Kobaron (Site 5, not surveyed in the first two samplings). Sites 1-4 were arranged following the pollution gradient. Site 5 was a control site. A non-destructive sampling strategy was implemented which consisted of visually assessed estimates of algal abundance at specific levels following the abundance-covering scale proposed by Braun-Blanquet (1951): + (<1% cover); 1 (1-5%); 2 (5-25%); 3 (25-50%); 4 (50-75%); 5 (75-100%). Five replicate quadrats (0.5 m^{-2}) on comparable flat or slightly sloped hard substrate surfaces were sampled at two intertidal levels (0.75 m: potentially dominated by Stypocaulon scoparium, and 1.4 m: potentially dominated by Corallina elongata). Species richness significantly increased throughout the study area during the period studied, whereas diversity showed different trends depending on the tidal level. Moreover, pollution removal promoted the development of morphologically more complex species. Resemblance between intertidal vegetation at the degraded sites and that of the reference site progressively increased. On the basis of non-metric



Fig. 1. Location of the study area and sites.

multidimensional scaling (nMDS) of Bray–Curtis similarities, computed using the species cover data matrix, five recovery stages were distinguished (Díez et al., 2009). The current study checks whether the above results can be obtained using reduced datasets.

The full species cover dataset was transformed to simulate coarse resolution samplings. Four factors were checked as potential sources of variation in the final results: (1) taxonomic aggregation level; (2) aggregation of species abundances into functional groups; (3) removal of occasional species; and (4) data transformation.

New data matrices were constructed by aggregating data into higher taxonomic levels for each replicate. Abundance measurements for taxa were sequentially summed to the appropriate taxon level (e.g. species into genera, genera into families, families into orders, and finally orders into classes) following the AlgaeBase classification (Guiry and Guiry, 2009).

A similar treatment was applied to simulate sampling of morphological functional group data. For each replicate, intertidal level and sampling site species cover data were aggregated into 10 algal morphological functional groups following a modified version of the scheme proposed by Steneck and Dethier (1994). Erect species were classified into nine groups: (1) filamentous (uniseriate); (2) polysiphonated; (3) foliose non-corticated (one or two layers); (4) foliose corticated; (5) terete slightly corticated (cortex with two layers); (6) terete corticated; (7) leathery; (8) articulated calcareous; (9) crustose calcareous; and (10) crustose non-calcareous species.

Intertidal vegetation usually comprises a few dominant macrophytes, several accompanying species and a relatively large percentage of occasional algae (cover = 0.5%). 'In situ' detection and identification of these latter species are highly time consuming, so we explored the effect of removing them from the full species dataset. Occasional algae records represented 56% of the total records for the 0.75 m tidal level and 55% for the 1.40 m tidal level.

Finally, each dataset was subjected to a sequence of transformations that gradually decreased the influence of dominant taxa: square root, $\log (x + 1)$ and presence/absence transformations.

Taxa richness (S), defined as the number of taxa per quadrat, taxonomic diversity measured with the Shannon–Wiener H' (loge based index) and Simpson $(1 - \lambda)$ diversity indices and the evenness of distribution between taxa expressed by the Pielou J' index were calculated for the reference and reduced datasets. The correlations between these community measures were determined using Pearson correlation. Prior to the analyses it was checked that the relationships between pairs of variables were linear by means of scatterplots.

Spatio-temporal patterns in phytobenthic assemblages based on the different data treatments were explored by performing non-parametric multidimensional scaling (nMDS) ordinations. Similarities between samples were calculated for each matrix by applying the Bray–Curtis similarity index (Bray and Curtis, 1957).

The similarity of the reference data set (square-root transformed species-level dataset) to each of the reduced datasets was gauged using second-stage nMDS (Somerfield and Clarke, 1995; Clarke et al., 2006). This procedure generates a correlation between each pair of similarity matrices to produce a derived similarity matrix that is itself subject to ordination. The resulting plot gives an objective comparison between the matrices. Resemblances among all matrices were determined by the Spearman rank correlation coefficient.

Subsequently, non-metric multidimensional scaling (nMDS) analyses were performed on those similarity matrices more closely related regarding Spearman rank correlation coefficient results. We thus visually explored the effect of each data treatment on the detection of the recovery process, which in the species-level ordi-

nation is reflected by a temporal displacement of the degraded sites towards the reference site. Statistical analyses were carried out using the PRIMER-E statistical package (Clarke and Warwick, 2001).

3. Results

3.1. Patterns of distribution

Second-stage nMDS ordination plots (Fig. 2) show the relationship between the various analysis options and the reference datasets (based on square-root transformed full species abundances: SpSR). For both intertidal assemblages studied (Fig. 2A and B), diagrams show that matrices based on class and morphological functional group abundances and those based on strongly transformed data (presence/absence) capture information on phytobenthos distribution patterns that is quite different from that of the reference datasets.

Subsequent 2nd-stage nMDS ordinations resulting from leaving out the most different matrices reveal two gradients (Fig. 3A and B): the effect of transformation from none to $\log(x + 1)$ and the effect of taxonomic aggregation from species to orders. The effect of transformation is only lower at species level for the 0.75 m assemblages. Matrices derived from full species datasets and those obtained by removing species with low cover (cover = 0.5%) using the same transformation tend to cluster together, indicating that removing occasional species has less effect on the outcome of these analyses than the other factors. The most similar matrices to the reference ones (SpSR) are those based on log(x + 1) transformed species abundances (SpLog), square root and log(x + 1) transformed species abundances without occasional species (Sp*SR, Sp*Log) and those obtained from square-root transformed genus abundances (GSR). These similarity matrices have Spearman rank correlations above $\rho > 0.95$ (Fig. 4).

The nMDS plots of Figs. 5 and 6 show the effects of using species, genus, family and order abundance data and datasets without occasional species in detecting spatio-temporal trends in the structure of the vegetation studied. The displacement of each site with respect to its initial position reflects the changes in the community's structure over time, from 1984 to 2008. A pollution gradient is detected from right to left in all diagrams. At the beginning of the study, the most degraded sites (Sites 1 and 2) were on the right, with Sites 3 and 4 being located between the most degraded sites and the control site (Site 5). A net displacement of all the sites towards the control site is evident. In the ordination plots of the reference study (Díez et al., 2009) five levels of degradation (extreme, heavy, moderate, slight and control) were differentiated by dividing the pollution gradient into five parts as it is showed in SpSR plots of Figs. 5 and 6. With regards to this classification, the distribution of samples is visually almost identical on the nMDS plots created from similarity matrices based on full species log(x + 1)transformed abundances data (SpLog), species abundance data without occasional species (Sp*SR, Sp*Log) and genus abundances (GSR, GLog). Ordination plots derived from similarity matrices based on family (FSR) and order (OSR) abundance data capture slightly different information. Although the net displacement of the polluted sites towards the control site remains clear, substantial differences can be appreciated. Thus, assemblages from Site 1 that were extremely degraded in 1984 and became moderately degraded at the end of study in the reference plot reached slightly degraded status according to the plots based on family and order similarity matrices. In general, the discrimination between slightly and moderately degraded communities becomes more confusing when higher taxonomic levels are applied. On the other hand, lower data resolutions resulted in patterns visually more similar to the reference nMDS plot (SpSR plot) in the case of assemblages from



Fig. 2. 'Second-stage' non-metric multidimensional scaling (nMDS) ordinations of inter-matrix rank correlations between a full species data matrix and the matrix resulting from removing occasional taxa (Sp*) and the matrices based on reduced datasets constructed by the aggregation of species data (Sp) into higher taxonomic levels: genus (G), family (F), order (O), class (C) and morphological functional groups (FG), in combination with different transformations of abundances (NT: no transform, SR: square-root, Log: log (x + 1), PA: presence/absence). A: 1.4 m tidal level; B: 0.75 m tidal level. White circle: reference dataset (full species abundances square-root transformed). Points inside the dashed oval correspond to resemblance matrices derived from species, genus, family and order abundance data with the following transformation treatments: no transform, square-root and log (x + 1).



Fig. 3. 'Second-stage' non-metric multidimensional scaling (nMDS) ordinations resulting from removing matrices based on classes, presence/absence and functional group datasets. For each transformation treatment consecutive levels of taxonomic aggregation are linked with a line. Labels of the various treatments applied: Sp = species; $(Sp^*) = removal of occasional species; G = genera, F = families, O = orders; NT = no transform; SR = square-root; Log = log (x + 1). (A) (1.4 m tidal level): Kruskal stress = 0.04; (B) (0.75 m tidal level): Kruskal stress = 0.07.$



Fig. 4. Pair-wise Spearman rank correlations (ρ) between the reference resemblance matrix (SpSR) and matrices derived from reduced datasets constructed by the removal of occasional species (Sp*) and the aggregation of species data (Sp) into higher taxonomic levels: genus (G), family (F) and order (O) in combination with different transformations of abundances (NT: no transform, SR: square-root, Log: log (x + 1)). Black circles: 0.75 m tidal level; White circles: 1.4 m tidal level.

the lowest tidal level (Fig. 6), as may be expected in view of the higher Spearman rank correlations between all pairs of similarity matrices obtained for these communities (Fig. 4).

With regards to species composition, vegetation at the degraded sites became progressively more similar to that of the reference site as it is shown in the ordination analyses derived from presence/absence data (Fig. 7). These sample shifts towards the control site are still evident when rare species are removed from datasets. However, Spearman rank correlations between similarity matrices based on full species dataset and those obtained by removing occasional species (high tidal level: $\rho > 0.70$; low tidal level: $\rho > 0.79$) indicate certain loss of information.

3.2. Patterns of diversity

Considering Sites 1, 2, 3 and 4 (the polluted area) together, the number of species increased during the period studied (1984–2008) from 38 to 84, genera from 28 to 61, families from 19 to 30 and orders from 12 to 17 (Table 1).

For both tidal levels, species richness was significantly correlated (*p*-value < 0.001) with all richness measures calculated on the basis of reduced datasets, though the strength of correlation varied from one to another (Table 2). Genus richness is the measure that most properly reflects the species richness patterns over time (r = 0.985 and 0.977, for 1.4 m and 0.75 m assemblages, respectively) (Table 2; Fig. 8A and B). Genera contained a low and fairly constant number of species per sampling unit over time:



Fig. 5. nMDS ordination plots of Bray–Curtis similarities based on species (Sp), genus (G), family (F) and order (O) abundances showing the separation of 1.4 m tidal level assemblages according to sites and time of sampling. Lines reflect the displacement of each site with respect to its initial position (from 1984 to 2008). (Sp*) data without occasional species. Type of data transformation: SR (square root); Log (log (x + 1)). Broken lines are only visual references to facilitate the comparison between surrogate plots and the reference plot (SpSR).

1.1 in most cases (Table 3). Family and order richness were not such good surrogates of species richness variation, since the ratios

of the number of species to the number of families and orders were more variable over time (Table 3), although the increasing trend



Fig. 6. nMDS ordination plots of Bray–Curtis similarities based on species (Sp), genus (G), family (F) and order (O) abundances showing the separation of 0.75 m tidal level assemblages according to sites and time of sampling. Lines reflect the displacement of each site with respect to its initial position (from 1984 to 2008). (Sp*) data without occasional species. Type of data transformation: SR (square root); Log (log (x + 1)). Broken lines are only visual references to facilitate the comparison between surrogate plots and the reference plot (SpSR).

was still evident (Fig. 8A and B). Finally, changes in species richness without considering occasional species did not properly match the

full species richness variation. This latter result reflects that the entry of rare species into the assemblages was highly variable from 1



Fig. 7. nMDS ordination plots of Bray–Curtis similarities based on qualitative information (PA: presence/absence) of the full species data set (Sp) and data set without occasional species (Sp*). Lines reflect the displacement of each site with respect to its initial position (from 1984 to 2008). (A): 1.4 m tidal level; (B): 0.75 m tidal level.

Table 1

Variation in the total number of species (Sp), genera (G), Families (F) and orders (O) considering the polluted area (Sites 1, 2, 3 and 4 together) over the period 1984–2008 and both tidal levels.

	1984	1992	1996	1998	2000	2002	2004	2006	2008
Species (Sp)	38	36	58	66	58	62	87	74	84
Genera (G)	28	27	45	52	47	47	62	57	61
Families (F)	19	18	26	28	27	28	33	31	30
Orders (O)	12	12	14	16	16	16	16	17	17

Table 2

Pearson correlations between diversity measures (*S*: number of taxa per quadrat, *H*': Shannon–Wiener index, *D*: Simpson (1 - l') index, *J*': Pielou's evenness) of reference dataset comprising all taxa identified to species level (Sp) and the reduced datasets constructed for higher taxonomic levels: genera (G), families (F) and orders (O) and by removing occasional species (Sp'; *p*-value < 0.001 in all cases.

	1.4 m assemblages				0.75 m assemblages				
	S	H′	D	J′	S	H′	D	J'	
Sp-Sp* Sp-G Sp-F Sp-O	0.763 0.985 0.916 0.875	0.982 0.976 0.908 0.900	0.995 0.986 0.915 0.914	0.950 0.973 0.926 0.900	0.590 0.977 0.891 0.814	0.964 0.967 0.850 0.821	0.995 0.984 0.861 0.857	0.768 0.955 0.819 0.794	

0.75 m tidal level and those at 1.4 m in the degree of correlation between diversity measures, with the highest tidal level showing the strongest correlations: r > 0.9 in all cases (Table 2). In the case of the lowest tidal level, the correlations between the reference dataset and those constructed for families and orders were only moderate (r > 0.8), but they still reflect the general trend. Changes in diversity omitting occasional species properly reflect the full species variation for both tidal levels (Figs. 9 and 10). Of the surrogate measures, changes in genus evenness is the most closely related to species evenness variation (Table 2; Fig. 11), but the remaining measures still fit it properly in most cases.

4. Discussion

year to another, and was largely responsible for the increasing trend detected in full species richness.

Diversity measures (both the Shannon–Wiener H' index (highly sensitive to the species richness) and Simpson $(1 - \lambda)$ index (less sensitive to the number of species)) showed a close relationship between the full species dataset and those calculated from higher taxa levels (Figs. 9 and 10). All correlations were significant at *p*-value < 0.001. There were differences between the assemblages at



Fig. 8. Mean values of taxonomic richness derived from full species data set (Sp), species data set after the removal of occasional species (Sp*), and taxonomically aggregated data: G (genera), F (families) and O (orders) in different years of sampling during the period 1984–2008. Means ± standard error are plotted. Lines between points are included for the sake of clarity and do not imply a continuous relationship between years of sampling. A: 1.4 m tidal level; B: 0.75 m tidal level.

although they may not reveal differences between moderately and slightly degraded communities. Likewise, diversity measures based on higher taxa (genus and family) adequately reflect changes in species richness and diversity during the period studied.

These results concur with the increasing evidence that lowerthat-species levels of taxonomic resolution are sufficient for detecting differences in benthic community structure. Taxonomic sufficiency seems to be particularly useful in detecting disturbance effects on soft bottom (Ferraro and Cole, 1990; Somerfield and Clarke, 1995; Olsgard et al., 1997; De Biasi et al., 2003; Gomez-Gesteira et al., 2003; Thompson et al., 2003; Sánchez-Moyano et al., 2006; Tataranni et al., 2009) and rocky macrofaunal assemblages (Urkiaga-Alberdi et al., 1999; Pagola-Carte et al., 2002; Lasiak, 2003). Most surrogacy publications concerned with pollution gradients suggest that family level is the best surrogate descriptor for discriminating assemblage patterns.

The use of coarser taxonomic resolution was first explored to detect pollution gradients (Warwick, 1988; Craig et al., 1993), but it has also been successfully applied in analyzing natural environmental gradients (James et al., 1995; De Biasi et al., 2003; Lasiak, 2003; Włodarska-Kowalczuk and Kedra, 2007). In both cases, the strength of the gradient might influence the potentially sufficient taxonomical level for detecting changes. Ferraro and Cole (1990) suggest that a systematic hierarchy of community response occurs when stress increases. Therefore, depending on the degree of environmental degradation, different taxonomic levels might be more suitable. Olsgard and Somerfield (2000) for example, point out that family data is only useful for monitoring changes when the community structure results from a strong spatial gradient such as that induced by heavy pollution. Our results show that the effectiveness of taxonomic aggregation becomes progressively lower as intersample similarities increase. Consequently, discrimination between moderately and slightly degraded communities begins to be unclear at family level. However, Dethier and Schoch (2006) suggest that even a weak estuarine gradient might drive changes in assemblage composition at family level. In general, the ability of TS to recognise patterns increases when communities have a high percentage of families represented by a single species (Giangrande et al., 2005; Dethier and Schoch, 2006; Bates et al., 2007; Puente and Juanes, 2008; Tataranni et al., 2009). In those cases, the shift of families or genera along the environmental gradient may be expected to closely fit changes in species composition even if the gradient is small.

The applicability of TS in marine vegetation remains poorly studied in comparison with faunal assemblages (Puente and Juanes, 2008). However, the use of coarse taxonomic resolutions would be particularly useful since algal diversity can be exceptionally high in some habitats and the successful identification of some species requires not only considerable taxonomic expertise but also the presence of fertile reproductive structures (Hirst, 2006). Contrasting outcomes emerge from studies that have explored the effects of taxonomic resolution in discriminating macroalgal communities. Bates et al. (2007) find that mild reductions (i.e. to genus or family level) are able to resolve patterns of difference in intertidal vegetation structure. These results are consistent with those of Puente and Juanes (2008), who find that genus and family aggregation does not greatly alter the results obtained with the species data set. In the same way, Sánchez-Moyano et al. (2006) report high correlations between species and family levels in their analysis of the spatial variation of the epiphytic communities of the alga S. scoparium (L.) Kütz. By contrast, Hirst (2006) finds that aggregation of macroalgal biomass to higher taxonomic levels is substantially less informative than species data. He argues that subtidal benthic macroalgal communities in southern Australia are dominated by several species belonging to the same order, the order Fucales. The aggregation of species data into genus level

Table 3

Mean ratio of the number of species to the number of higher taxa (G = genera; F = families; O = orders) and to the number of species without occasionals (Sp*) per sample over time (from 1984 to 2008) for the two assemblages studied (1.4 m and 0.75 m tidal levels). The standard deviation is in parentheses.

	1984	1992	1996	1998	2000	2002	2004	2006	2008
1.4 m tidal level									
Sp/G	1.2 (0.1)	1.1 (0.1)	1.0 (0.1)	1.1 (0.0)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.0)	1.1 (0.1)
Sp/F	1.3 (0.2)	1.2 (0.2)	1.3 (0.2)	1.4 (0.1)	1.4 (0.2)	1.3 (0.1)	1.4 (0.2)	1.4 (0.2)	1.4 (0.3)
Sp/O	1.6 (0.4)	1.5 (0.4)	1.7 (0.3)	1.9 (0.2)	1.8 (0.2)	1.6 (0.2)	1.9 (0.4)	2.0 (0.4)	1.9 (0.4)
Sp/Sp*	1.6 (0.5)	1.9 (0.5)	2.5 (1.1)	2.3 (0.5)	2.0 (0.5)	2.2 (0.6)	2.5 (0.8)	2.8 (0.8)	2.2 (0.5)
0.75 m tidal level									
Sp/G	1.2 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)	1.1 (0.1)
Sp/F	1.5 (0.3)	1.3 (0.2)	1.5 (0.2)	1.5 (0.1)	1.5 (0.2)	1.4 (0.2)	1.6 (0.3)	1.6 (0.2)	1.6 (0.2)
Sp/O	1.7 (0.5)	1.6 (0.3)	2.1 (0.4)	2.1 (0.3)	2.1 (0.3)	1.8 (0.3)	2.2 (0.4)	2.2 (0.3)	2.3 (0.4)
Sp/Sp*	1.9 (0.4)	2.1 (0.5)	2.0 (0.5)	2.4 (0.6)	2.3 (1.0)	2.5 (0.6)	2.6 (0.7)	2.7 (0.5)	2.5 (0.6)



Fig. 9. Mean values of Shannon–Wiener Diversity (H') derived from full species data set (Sp), species data set after the removal of occasional species (Sp*), and taxonomically aggregated data: G (genera), F (families) and O (orders) in different years of sampling between 1984 and 2008. Means ± standard error are plotted. Lines between points are included only to aid interpretation, and imply no relationship in diversity values between years of sampling. A: 1.4 m tidal level; B: 0.75 m tidal level.

and subsequently into family level alters the dominance patterns and this, in turn, alters the outcome of the analyses. On exploring the influence of higher taxonomic resolution in detecting differences among macroalgal assemblages from three regions of the Gulf of Alaska, Konar and Iken (2009) find that intertidal communities could be discerned at all taxonomic levels, whereas for subtidal vegetation taxonomic surrogates are not so appropriate. The discrepancies arising from the studies mentioned above have raised an issue that has been underlined by several authors (Olsgard and Somerfield, 2000; Terlizzi et al., 2003; Bates et al., 2007) that is, before applying 'taxonomic sufficiency' it is necessary to carry out baseline studies at high-resolution level because the knowledge of species is a prerequisite for defining the potentially sufficient taxonomical level.

Another relevant topic dealt with in this work is the effect of the interaction between taxonomic level and type of transformation. The choice of transformation is a biological decision that determines the contribution of dominant, mid-abundance and rare species in the outcomes of multivariate analyses. Ordinations on untransformed data reflect the distribution patterns of dominant taxa, whereas analyses based on strong transformed data, such as $\log(x + 1)$ or 4th-root transformed data, focus their attention within the whole community (Clarke and Warwick, 2001). Several studies have found that as the severity of transformations becomes higher, so the loss of information using higher taxonomic levels increases (Olsgard et al., 1998; Anderson et al., 2005a; Puente and Juanes, 2008); therefore, the most appropriate taxonomic aggregation level might vary depending on which aspect of the community is the target of the study (Olsgard et al., 1998; Karakassis and Hatziyanni, 2000; Lasiak, 2003). Our results partially concur with



Fig. 10. Mean values of Simpson $(1 - \lambda)$ diversity derived from full species data set (Sp), species data set after the removal of occasional species (Sp*), and taxonomically aggregated data: G (genera), F (families) and O (orders) in different years of sampling between 1984 and 2008. Means ± standard error are plotted. Lines between points are included only to aid interpretation, and imply no relationship in diversity values between years of sampling. A: 1.4 m tidal level; B: 0.75 m tidal level.

these findings. For assemblages from 1.4 m tidal level (potential community of *C. elongata*) the effects of taxonomic aggregation are lower when species data are not transformed. However, for assemblages from 0.75 m tidal level (potential community of *S. scoparium*) taxonomic aggregation level has similar effects regardless of the transformations. The interaction between data transformation and taxonomic sufficiency appears to depend largely on the dataset structure, so when designing a study its effect should be always examined before selecting a possible taxonomic level.

The use of only data on conspicuous species (cover higher than 1%) has also been checked as a potential source of variation in the final results of the present study. Out of all the data resolution reduction approaches this works best for detecting assemblage distribution in the case of quantitative data. Hardly any information is lost when these occasional algae are not considered. The benefits of using this sampling resolution appear to be substantial since it allows a 50% reduction in the number of records to be viewed on site in the field and in the subsequent task of identifying a large percentage of them in the laboratory. Our results are consistent with the conclusions of Puente and Juanes (2008), who analyse the suitability of using subsets of representative species for assessing macroalgal assemblages using reduced matrices created by removing species with low biomass (minimum weight 0.5 g dw m^{-2}). They found that this reduced sampling resolution approach is a good alternative to the use of a full species dataset, taking into account the balance between accuracy and processing effort. The findings mentioned above indicate that it is not necessary to record all species present in the community when the aim of the study is to discriminate marine phytobenthic assemblages on the basis of quantitative data. However, as emerges from our study, when anal-



Fig. 11. Mean values of Pielou evenness (*I*') derived from full species data set (Sp), species data set after the removal of occasional species (Sp*), and taxonomically aggregated data: G (genera), F (families) and O (orders) in different years of sampling between 1984 and 2008. Means \pm standard error are plotted. Lines between points are included only to aid interpretation, and imply no relationship in evenness values between years of sampling. A: 1.4 m tidal level; B: 0.75 m tidal level.

yses are focussed in detecting differences in species composition, that is, when they are based on presence/absence data, certain information is lost if rare species are removed.

It has also been found in the current study that matrices based on morphological functional groups data capture quite different information on spatio-temporal distribution of phytobenthos from matrices based on species data. Discrepancies emerge in regard to previous studies dealing with the applicability of methods based on morphological functional groups of macroalgae as a data simplification approach for reducing sampling effort (Phillips et al., 1997; Tobin et al., 1998; Bates et al., 2007). Konar and Iken (2009) find this reduced data resolution useful for distinguishing phytobenthic assemblages at a regional scale, for both intertidal and subtidal communities. Likewise, Tobin et al. (1998) suggest that functional composition could more successfully discriminate sites than species-level information. However, Bates et al. (2007) find that this approach does not yield results consistent with high-resolution data; they find its performance comparable to the use of a species list. In the same way, Phillips et al. (1997) concludes that the use of functional groups results in considerable loss of information. The disagreements in the conclusions derived from these studies could be partially related to differences in the morphological classification scheme adopted by them.

With regard to diversity, our results reveal that all surrogate measures properly match changes in Shannon and Simpson measures, as well as Pielou's evenness. By contrast, species richness variation is only appropriately reflected by data aggregated into genera and families. Given that out of the diversity measures presented here, species richness is the best descriptor of the recovery process experienced by the intertidal vegetation targeted in the current study, we recommend using genus data instead of removing occasional species for detecting changes in diversity as result of water improvement. Positive correlations between species richness and higher taxon richness have been found for a variety of habitats (Vanderklift et al., 1996; Doerries and Van Dover, 2003), particularly when the number of species in each higher taxon is low (Włodarska-Kowalczuk and Kedra, 2007), as it is in our study, where the ratio of number of species to number of genera is close to 1. In these cases, the savings in time and effort are be limited, and it seems more useful to count species directly (Gaston, 2000). However, the use of higher taxon surrogates might still be appropriate because the number of species because identification at species level implies a higher probability of error (Guzmán-Alvis and Carrasco, 2005; Dethier and Schoch, 2006; Bates et al., 2007).

From the results that we present here the following conclusions can be drawn: (1) if collecting data at species level is not feasible, genus data is the most appropriate taxonomic surrogate for discriminating macroalgal assemblages and detecting changes in diversity; (2) morphological functional groups are not considered a suitable option for reflecting the spatio-temporal variation of species; (3) the use of only conspicuous taxa allows patterns of change in communities to be identified but it is not a good alternative for representing full species richness variation; (4) although this study reveals only a slight interaction between taxonomic sufficiency and data transformation, this relationship should be examined beforehand to decide which taxonomic level performs best; and (5) before applying reduced sampling resolution approaches baseline studies at species level should be performed.

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