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Influence of taxonomic resolution on multivariate analyses of arthropod and macroalgal reef assemblages

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ABSTRACT: There are currently few recommendations regarding the taxonomic resolution required to sufficiently describe patterns of community structure among temperate rocky-reef invertebrate and macroalgal assemblages. Studies conducted in a range of other aquatic systems have indicated that there is a high degree of redundant information conveyed at the species level, in comparison to higher taxonomic levels. This has important implications for the design of many ecological studies in terms of the allocation of resources. This study examined the impact of taxonomic aggregation on the detection of multivariate patterns in faunal and macroalgal assemblage structure amongst temperate subtidal reef communities in southern Australia. I considered the level at which taxonomic aggregation led to the loss of resolution in multivariate patterns, impairing conclusions regarding assemblage patterns at the species level. This study 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 species-level identifications, aggregation of macroalgal data to higher taxonomic levels was substantially less informative. Thus, whereas significant cost-savings can be achieved by identifying invertebrate taxa to family with little or no loss of information, the same is not true for macroalgal assemblages. Differences between faunal and algal assemblages were attributable in part to the distribution of species within higher taxa. In particular, the aggregation of macroalgal species belonging to the order Fucales (e.g. *Sargassum*, *Cystophora* etc.) resulted in impaired representation of assemblages in multivariate patterns, as a consequence of the diversity, dominance and wide distribution of this order within benthic macroalgal groups of southern Australia.

KEY WORDS: Taxonomic resolution · Temperate rocky reef assemblages · Southern Australia · Amphipods · Fucoids · BVSTEP analysis

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INTRODUCTION

One of the major costs associated with surveying benthic aquatic environments is the time required to identify biological specimens. This cost can vary dramatically depending on the level of taxonomic resolution used. In a study of soft-bottom communities from the Southern Californian Bight, Ferraro & Cole (1995) found that species-level identifications were double the cost of family-level identifications and almost 5 times the cost of order-level identifications. Until relatively recently, it was believed that the increased cost of identifying specimens to species was offset by greater sensitivity and resolution in detecting changes in marine communities. However, there is increasing evidence that quite low levels of taxonomic resolution (i.e. order or phylum) are sufficient for the detection of impacts on the marine environment (Warwick

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1988a,b). Moreover, even broad-scale regional patterns can be detected using phylum-level identifications (Lasiak 2003) or at the very least, data aggregated to the family level (Hewlett 2000). These findings have important implications for the design of future sampling programs because they suggest that, by adopting a coarser taxonomic level identification, similar outcomes may be achieved with reduced sample processing costs.

Interestingly, the results of these studies indicate that, depending on the scope of the question addressed, there is considerable redundancy in relation to the distribution and behaviour of taxa discriminated at lower (i.e. species, genus) in comparison to higher taxonomic levels (i.e. order, phylum). In particular, where there are major environmental or disturbance gradients, similar patterns may still be evident when taxa are aggregated at widely differing taxonomic levels (Warwick 1988a,b, Somerfield & Clarke 1995). Warwick (1988a,b, 1993) has suggested that taxonomic levels higher than species may actually be of greater value in detecting human impacts because individual species' abundances are more likely to be complicated by natural environmental heterogeneity. Olsgard et al. (1998) showed that the level of concordance in multivariate patterns between species and higher taxonomic levels varies with the extent of the disturbance gradient. They found that the level of congruence between species-level data sets and data sets aggregated to a coarser taxonomic level was greater for macrofaunal communities disturbed by pollution in comparison to more pristine environments. This phenomenon may be a consequence of the hierarchical nature of biological responses to stress (Pearson & Rosenberg 1978), whereby impacts resulting from increased anthropogenic stress are manifested at higher and higher taxonomic levels (i.e. sensitivity to stress is phylogenetically related). However, even for communities largely free of anthropogenic impacts, aggregation of data to the family level has been found to produce results, which in most cases (Metzeling et al. 2002 is a single exception) were largely inseparable from analyses based on species-level identifications (James et al. 1995, Marchant et al. 1995, Olsgard et al. 1998, Hewlett 2000).

The degree to which anthropogenic impacts can be detected using coarser taxonomic resolution has been widely documented among soft bottom (Ferrero & Cole 1995, Somerfield & Clarke 1995, Vanderklift et al. 1996, Olsgard et al. 1997, Stark et al. 2003) and other benthic marine environments (Smith & Simpson 1993, Lasiak 2003, Anderson et al. 2005a). Fewer studies have examined the extent to which taxonomic resolution influences the detection of natural patterns and gradients in community structure among unimpacted benthic environments, despite the potential time and cost savings that may be accrued. Moreover, there are few recommendations regarding the taxonomic resolution required to sufficiently describe patterns of community structure among subtidal rocky-reef invertebrate and macroalgal communities. Somerfield & Clarke (1995) suggest that the extent to which aggregation to higher taxonomic levels influences the resulting analyses depends ultimately on the distribution of species among higher taxa. They found that, in general, aggregation to higher taxonomic levels was less effective for analyses of more diverse communities, compared to less diverse communities. This is because aggregating phylogenetically rich (in comparison to phylogenetically poor) groups results in a potentially greater degree of information loss.

The influence of varying levels of taxonomic resolution on the identification of multivariate assemblage patterns amongst shallow (<12 m) subtidal rocky reef communities from localities free of major human impacts was examined in this study by amalgamating species-level data for phytal epifaunal arthropods (crustaceans and pycnogonids) and macroalgae sampled from rocky reef environments at the genus, family, order and phylum (for algae only) levels. Epiphytal arthropod and macroalgal communities from southern Australia are very diverse (Barnard 1972, 1974, Womersley 1984) and include a number of species-rich groups (e.g. dexaminid and ampithoid amphipods; sphaeromatid isopods and fucoid brown algae). Thus, these groups provide a robust examination of the merits of using coarse taxonomic resolution to describe spatial patterns in assemblage structure. This study specifically considers the extent to which patterns inherent at the species level were detectable for invertebrate and macroalgal assemblages aggregated at courser taxonomic levels, using non-parametric multivariate statistical analyses. In stark comparison to the faunal assemblages, there are currently no published accounts of the merits of using higher taxonomic categories to describe macroalgal assemblage structure.

MATERIALS AND METHODS

Data. Three sets of species distribution data were used in this study: arthropod (>1.0 mm) species abundance and macroalgal species biomass data collected from 6 locations in the St. Francis Isles group in the Nuyts Archipelago (Hirst 2003) and arthropod faunal data collected from canopy and understorey algal assemblages among sites off the Fleurieu Peninsula, South Australia (Hirst in press) (Fig. 1)—hereafter referred to as the Nuyts faunal, Nuyts algal and Fleurieu faunal data sets, respectively.

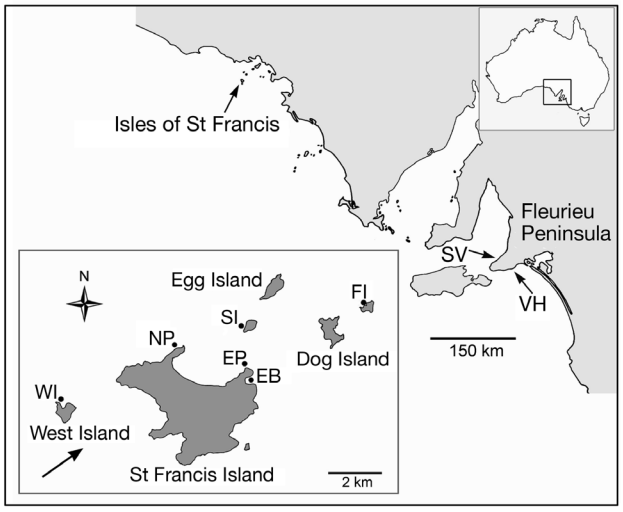

Fig. 1. Geographical location of the 2 data sets used in this study. SV: Second Valley; VH: Victor Harbour (Fleurieu Peninsula). Insert shows location of the 6 sites within the St. Francis Is. group (Nuyts Archipelago); EB: East Bay; EP: East Pt; FI: Freeling Is; NP: North Point; WI: West Island; arrow: direction of prevailing ocean swell

Study sites and field methods. The St. Francis Isles are a group of islands located approximately 40 km off the coast of the Australian mainland in the eastern part of the Great Australian Bight. The islands are remote, unpopulated and the nearest human population centre is over 50 km away (Ceduna, pop. ~2700). The islands are exposed to heavy oceanic swell from the Southern Ocean and both faunal and algal samples displayed a clear exposure gradient from protected to more exposed localities when analysed at the species level (Hirst 2003). The prevailing direction of the swell is from the south-west (Shepherd & Womersley 1976, NAVAIR 1969). Six sites were sampled in February 2002, spanning a range of macroalgal habitats and exposure to oceanic swell (Fig. 1). Low-relief reefs at East Point and East Bay, at the north-eastern corner of St Francis Island, supported mixed fucoid macroalgal communities, and are largely sheltered from the prevailing swell. These sites could always be dived during our visit, regardless of the conditions. Fucoid-dominated macroalgal communities at Freeling Island were located within a semi-protected, shallow embayment on the northern side of the island and are subject to moderate wave energy. *Scytothalia*- (Smooth Is. & North Pt) and *Ecklonia*- (West Is.) dominated macroalgal communities were found on more westerly facing rocky outcrops with greater inclination (reefs sloping abruptly to a depth of about 20 to 25 m) and exposure to oceanic swell.

The faunal assemblages from 2 locations (Second Valley and Victor Harbour) on the Fleurieu Peninsula displayed clear differences between adjacent canopy and understorey habitats when identified at the species level (Hirst in press). Both locations are coastal fringing reefs removed from obvious human impacts (i.e. sewage outfall, commercial fishing or habitat destruction).

Macroalgae and epiphytal faunal assemblages were sampled concurrently from haphazardly chosen 0.06 m^2 (25 × 25 cm) quadrats. In the case of the Nuyts samples, canopy algae (defined as algal species >10 cm height) were carefully removed from the substrate by hand or using a knife, and promptly placed into sealable 1 mm mesh bags. Kelp-like algae such as *Ecklonia radiata* or *Scytothalia dorycarpa* were removed above the holdfast. At each site, 10 replicate quadrats were collected at 10 m depth using SCUBA (further details in Hirst 2003). In the case of the Fleurieu study, adjacent canopy and understorey habitats (algae and associated epifauna) were sampled simultaneously in the field using 0.06 m^2 quadrats. Samples were collected in 2 stages: firstly, canopy vegetation (>10 cm height) was cut above the holdfast or rhizome and placed into 1 mm mesh collection bags. The remaining benthos (understorey) was then scraped physically from the rock and collected using an air-lift sampler into separate 1 mm mesh bags. Twenty complete samples (canopy and understorey) were collected from the Second Valley location and 18 from the Victor Harbour location. Further details are available in Hirst (in press). Fauna were separated from the algae through repeated washing in fresh water and all material retained on a 1.0 mm mesh sieve was initially fixed in 5% formalin in seawater and then later transferred to 70% ethanol. Mobile arthropod fauna (i.e. crustaceans and pycnogonids) were identified to the lowest possible taxonomic unit and enumerated for each sample. Algae were identified to species (where possible) and weighed following drying at 85°C for 48 h.

Eighty-four species of macrofauna and 34 species of macroalgae were collected during the survey of 6 sites in the St Francis Isles. The Fleurieu data comprised 93 arthropod species collected from canopy and understorey habitats at 2 locations (n = 78 samples) (Table 1). Few studies are able to identify all specimens to species and thus specimens were generally identified to the 'lowest taxonomic unit', commonly a mix of genus- and species-level identifications. For this study in excess of 70% of the Nuyts and Fleurieu faunal taxa were assigned species names or discriminated at the morphospecies level (i.e. morphologically distinct from other members of the genus). The remainder of the fauna were identified to genus or in some instances to family.

Data analyses. Arthropod species sample abundance data was aggregated at the level of genus, family and

order using taxonomic information contained within Barnard & Karaman (1991) and Lowry & Springthorpe (2001) for amphipods; the 'World List of Marine, Freshwater and Terrestrial Isopod Crustaceans' database (www.nmnh.si.edu/iz/isopod/) for isopods; Clark (1963) and Child (1988) for pycnogonids and Larsen (2002) for tanaids (family-level identifications only). Macroalgal species biomass was aggregated at the level of genus, family, order and phylum using nomenclature contained within Womersley (1984, 1987) for Phaeophyta and Chlorophyta; and the 'algaebase' database on the web (www.algaebase.org) for Rhodophyta.

Data sets compiled at different taxonomic levels were compared using the methods outlined in Somerfield & Clarke (1995). Sample similarity was calculated using the Bray-Curtis similarity index for $\log_e(x + 1)$ faunal abundance and $\sqrt{}$macroalgal biomass (dry weight). Similarity matrices were compared using the RELATE procedure in PRIMER (Clarke & Warwick 2001). The degree of separation in terms of assemblage similarity between sites was examined using one-way analysis of similarity (ANOSIM) tests for the Nuyts data, and 2-way crossed ANOSIM comparing both habitats and sites for the Fleurieu data (Clarke & Warwick 2001). The global ANOSIM-test (Global *R*) and corresponding pairwise comparisons were used to measure the degree to which site differences, inherent at the species level, were retained for data sets aggregated at higher taxonomic levels. The significance of these tests was determined via randomisation tests (n = 999 permutations). Data matrices aggregated at varying taxonomic levels are represented visually in 2 dimensions using non-metric multidimensional scaling (nMDS). The ordinations shown in this study are illustrative rather than statistical tests in their own right and greater weight is given to those analyses that are derived directly from the similarity matrices (e.g. RELATE, ANOSIM). In some cases, stress for the 2D ordinations is at the upper limits of what is considered an acceptable representation and ordinations should be interpreted cautiously.

BIOENV (Clarke & Ainsworth 1993) was used to examine the extent to which correlations between site exposure and faunal and macroalgal assemblage structure, previously identified at the species level in Hirst (2003), were retained at coarser taxonomic levels. BIOENV calculates the Spearman rank correlation (ρ) between a similarity matrix and the corresponding environmental data for each sample. Significance of correlation coefficients was tested via a permutation test (n = 999 permutations) using the PRIMER v6.0 software package. The 6 Nuyts sites were each assigned an exposure ranking between 1 and 4. These rankings were derived from those used by Shepherd & Brook (2003) to examine associations between exposure/water movement and reef fish assemblages in the Nuyts Archipelago for many of the same sites considered in this study. Sites most protected from oceanic swell originating predominantly from the south-west (see Fig. 1) were assigned a ranking of 1 (i.e. EB and EP) whereas the most exposed sites were assigned a ranking of 4 (NP and SI). Sites deemed to be either partially protected (FI) or partially exposed (WI) were accordingly assigned exposure rankings of 2 and 3, respectively.

The BVSTEP algorithm in PRIMER was used to identify sub-sets of both faunal and algal taxa that explained variation (initially ρ = 0.95) in the sample-to-sample relationships inherent among the full data set (essentially a RELATE–style correlation). The algorithm is based on a stepwise procedure whereby taxa are iteratively removed or included until 'a best selection model' can be reached (i.e. a sub-set of taxa that explain at least ρ = 0.95 of the variation in the full data set). A complete explanation of the BVSTEP algorithm can be found in Clarke & Warwick (1998, 2001). Clarke & Gorley (2001) recommend removing the taxa included in the 'best selection model' and searching for alternative models or sub-sets of taxa (i.e. 'next best selection model'), which may explain similar levels of variation (*sensu* Clarke & Warwick 1998). In this exercise I have recalculated the 'best selection model' by sequentially reducing rho (ρ) by 0.05 (i.e. 0.95, 0.90, 0.85 etc) until the 'next best selection model' explains a similar amount of variation in the full data set as the 'best selected model'. I undertook this process in order to identify taxa that make strong contributions to the multivariate patterns discussed here (i.e. essentially drive the multivariate patterns). This analysis was used to indicate where the aggregation of taxa may result in distortion of multivariate patterns, through the aggregation of species that appear to be important drivers of multivariate patterns, within higher taxa.

RESULTS

The faunal and algal data sets showed different trends, in terms of the degree of correlation between the Bray-Curtis similarity matrices, in relation to the aggregation of taxa (Fig. 2). Whilst faunal data sets aggregated at the genus and family levels retained much of the information present at the species level for both faunal data sets (ρ > 0.85), aggregating the macroalgal data at the genus (ρ = 0.683) and family level (ρ = 0.551) resulted in a much greater loss of information. In fact, faunal data aggregated at the generic level was largely indistinguishable from the species-level data (ρ = 0.957 (Nuyts); ρ = 0.996

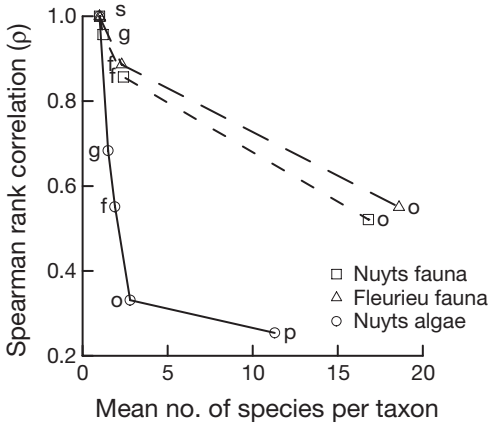

Fig. 2. Relationship between mean number of species per taxonomic group and the Spearman rank correlation coefficients (ρ) generated by comparing similarity matrices at higher taxonomic levels with the species-level similarity matrix; s: species; g: genus; f: family; o: order; p: phylum

Table 1. Faunal and macroalgal assemblages aggregated to species-, genus-, family-, order- and (Nuyts algae only) phylum-levels. Mean: mean no. of species per taxon

	Fleurieu fauna (n = 78)		Nuyts fauna (n = 57)		Nuyts algae (n = 57)	
	No. taxa	Mean	No. taxa	Mean	No. taxa	Mean
Species	93	1	84	1	34	1
Genus	90	1.03	69	1.2	22	1.5
Family	40	2.3	35	2.4	18	1.9
Order	5	18.6	5	16.8	12	2.8
Phylum					3	11.3

(Fleurieu)), perhaps in part because few genera contained more than a single species (Table 1). By comparison, the 22 genera amongst the algal data set contained only marginally more species per genus (i.e. 1.5 compared to 1.2 and 1.03, Table 1), but displayed only a modest correlation with the species data (Fig. 2). Similarity matrices aggregated at the order or phylum level were poorly correlated with the species matrices and in the case of the macroalgal samples retained little of the information present at the species level ($\rho < 0.33$).

The extent to which multivariate patterns in assemblage structure inherent at the species-level were retained amongst data sets aggregated at higher taxonomic levels was examined further using ANOSIM tests and MDS ordination. A pattern similar to that relayed by the Spearman rank correlations between similarity matrices was evident from the ordination of the Nuyts data (Figs. 3 & 4). Ordinations constructed at the species-, genus- and family-level for the faunal data showed a similar pattern (Fig. 3). Samples from EB and EP sites heavily overlapped, whereas samples from the NP site could be clearly distinguished from the other sites and appeared disparate in terms of assemblage composition. This pattern was less well defined at the order-level and this was reflected by a drop in the overall degree of separation between sites at this level (ANOSIM: Global $R = 0.272$ in comparison to Global $R = 0.428$ to 0.516 for family and below). Pairwise contrasts between sites largely supported this conclusion, as fewer sites could be distinguished after the faunal data was aggregated at the order-level (Table 2). Notably, a greater number of sites could be discriminated at the family-level (n = 14 significant pairwise contrasts) in comparison to the species-level assemblage data. Aggregation of macroalgal data to coarser levels of taxonomic resolution resulted in diminishing levels of separation between sites inherent at the species-level, compared to the faunal analyses (Table 2, Fig. 4). This corresponds with the marked decline in correlation between algal data sets aggregated at coarser taxonomic levels with the species data (Fig. 2). Phylum- and order-level algal data poorly represented patterns inherent at the species-level (Fig. 4). None of the 10 significant pairwise contrasts between sites formerly distinguishable at the species-level could be distinguished using algal assemblages aggregated at the phylum level (Table 2). Macroalgal data

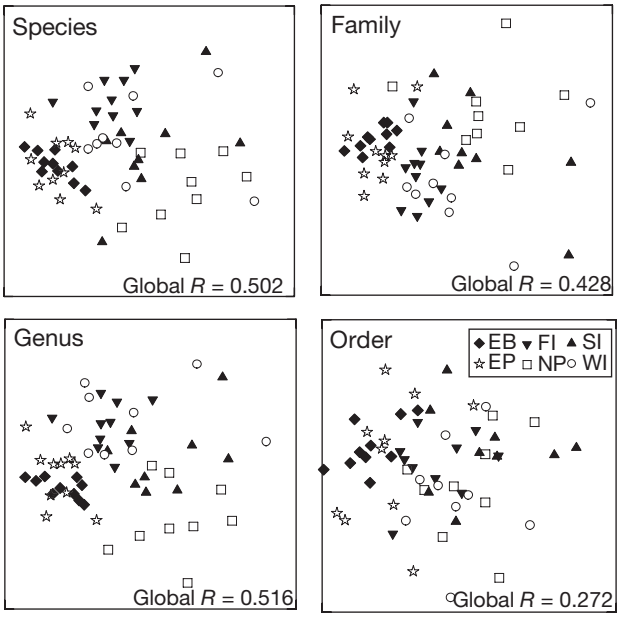

Fig. 3. MDS ordinations of $\log_e(x + 1)$ faunal abundance showing the location of Nuyts samples in 2-dimensional space for species- (stress = 0.22), genus- (stress = 0.23), family- (stress = 0.22) and order-level (stress = 0.18) similarity matrices. ANOSIM Global R statistics indicating the level of separation between all sites is displayed for each taxonomic level (see also Table 2). Sites as in Fig. 1

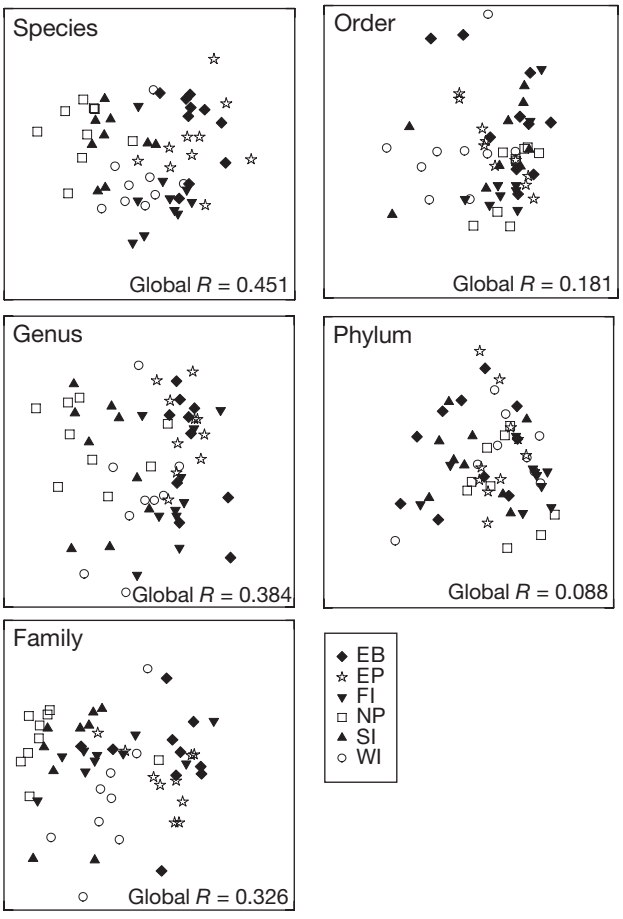

Fig. 4. MDS ordinations of √ transformed macroalgal biomass showing the location of Nuyts samples in 2-dimensional space for species- (stress = 0.16), genus- (stress = 0.19), family- (stress = 0.18), order- (stress = 0.20) and phylum-level (stress = 0.12) similarity matrices. ANOSIM Global *R* statistics indicating the level of separation between all sites is displayed for each taxonomic level (see also Table 2). Sites as in Fig. 1

aggregated to the order-level fared only slightly better (i.e. 2 out of 10, Table 2). Significant differences in faunal assemblage structure between habitats (canopy vs. understorey) and sites were evident at all taxonomic levels amongst the Fleurieu faunal data, although the overall pattern was not as clear at the order-level (Fig. 5) and the respective *R*-values were comparatively smaller (Table 3). However, all comparisons were significant at $p < 0.001$.

Correlations between site exposure and assemblage structure evident for the faunal (BIOENV, $\rho = 0.423$) and algal (BIOENV, $\rho = 0.464$) species assemblages were also retained at the genus and family levels (Fig. 6). When aggregated at the order-level, the correlation between site exposure and faunal assemblage structure was weaker (BIOENV, $\rho = 0.296$) but still statistically significant ($p < 0.001$). Correlations between

Table 2. Summary of 1-way ANOSIM tests between sites for the Nuyts faunal arthropod and algal data, aggregated to varying taxonomic levels. Range *R*: range of *R* values for pairwise contrasts between sites; Sig. contrasts: no. of contrasts found to be significant at $p < 0.003$, following correction for type 1 errors using a Bonferroni correction (for 6 sites there are a total of n = 15 contrasts between sites)

Taxonomic level	Global *R*	Range *R*	Sig. contrasts
Fauna			
Species	0.502	0.126 – 0.866	12
Genus	0.516	0.148 – 0.831	13
Family	0.428	0.182 – 0.747	14
Order	0.272	–0.076 – 0.727	7
Algae			
Species	0.451	0.027 – 0.838	10
Genus	0.384	0.001 – 0.715	9
Family	0.326	0.059 – 0.687	6
Order	0.181	–0.008 – 0.316	2
Phylum	0.088	–0.103 – 0.223	0

Table 3. Two-way crossed ANOSIM tests comparing habitats (canopy vs. understorey) and sites, for faunal abundance data aggregated to various taxonomic levels. All contrasts significant at $p < 0.001$

Taxonomic level	Source of variation	
	Habitat *R*	Site *R*
Species	0.400	0.703
Genus	0.398	0.703
Family	0.392	0.674
Order	0.344	0.542

site exposure and assemblage structure were not significant for macroalgal data aggregated to the order- and phylum-levels ($p > 0.05$) and the correlation coefficients were correspondingly small (Fig. 6).

BVSTEP analysis completed at the default $\rho = 0.95$ produced 'best selection' models comprising 16 faunal (Table 4) and 11 macroalgal taxa (Table 5). At reduced levels of ρ, the number of taxa retained within the 'best selection' model declined substantially to the point where only 5 taxa were required at $\rho = 0.80$ for both the faunal and algal data sets. Tables 4 and 5 showed that the important taxa (in terms of shaping multivariate patterns) were both abundant and common among the samples and sites. Overall, faunal taxa occurred more frequently among samples compared to macroalgal taxa. The most frequently collected single faunal taxon, *Tethygeneia nalgo*, was found in 42 of the 57 samples, whereas the most common algal taxon *Cystophora monilifera* was only found among 21 samples. Moreover, the 'best selection' taxa selected from the faunal and algal datasets differ considerably in

terms of their hierarchical taxonomic structure. Of the 16 faunal taxa in the 'best selection' model, only 2 taxa belonged to the same genus, *Ampithoe geographe* and *Ampithoe* spp. (comprising >2 species that were otherwise difficult to consistently distinguish). At the family-level, only 3 families contained more than a single species: ampithoid amphipods (3 taxa), eusirid amphipods (2) and sphaeromatid isopods (2). By comparison, the macroalgal 'best selection' model contained 5 species belonging to the genera *Sargassum*, and 7 taxa belonging to the order Fucales out of 11 selected taxa (Table 5). Taxonomic aggregation therefore has vastly different impacts on the way data at the species level is manifested at courser taxonomic levels for the faunal and algal data sets.

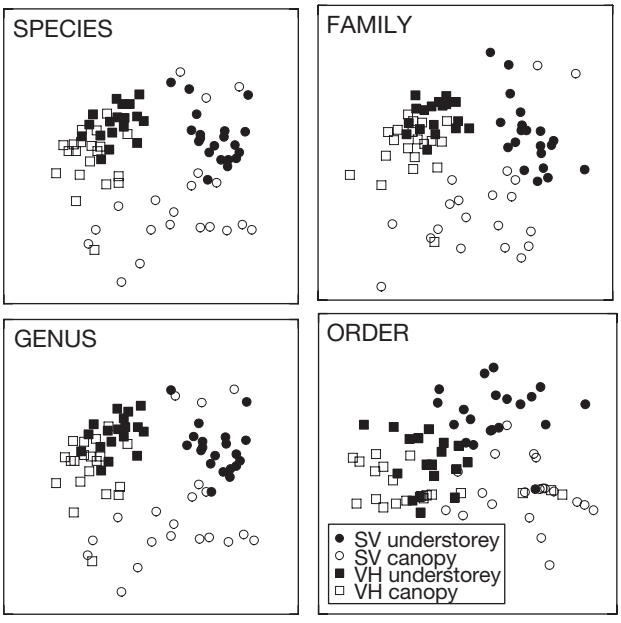

Fig. 5. MDS ordinations of $\log_e(x+1)$ faunal abundance showing the position of Fleurieu samples from sites (SV vs. VH) and habitats within sites (understorey vs. canopy) in 2-dimensional space for species (stress = 0.18), genus (stress = 0.18), family (stress = 0.18) and order (stress = 0.13) level similarity matrices

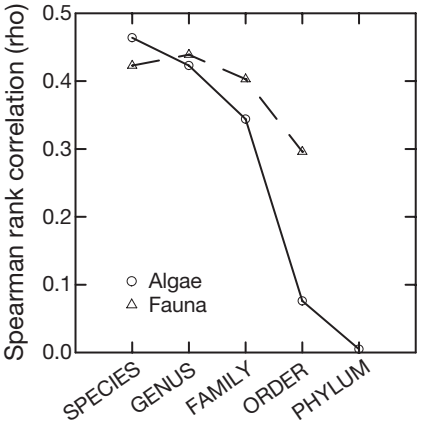

Fig. 6. BIOENV Spearman rank correlations (ρ) between site exposure and the Nuyts faunal and algal similarity matrices aggregated at varying taxonomic levels. Site exposure: categorical ranking ranging from 1 (protected) to 4 (exposed)

Table 4. BVSTEP analyses displaying sub-sets of Nuyts arthropod taxa comprising the best selection models at ρ = 0.95, 0.9, 0.85 and 0.8. At ρ = 0.8, the 'next best selection' model constitutes a viable alternative (i.e. ρ = 0.826). Taxa ranked by frequency of occurrence among samples. A: Amphipoda; I: Isopoda; T: Tanaidacea; *out of n = 57 samples; **out of n = 6 sites

Taxonomic name	Family	Order	Present in no. of samples*	sites**	Total abundance	Absent from sites:	ρ 0.95	0.9	0.85	0.8
Aoridae spp.	Aoridae	A	50	6	426		x	x	x	x
Tethygeneia nalgo	Eusiridae	A	42	6	272		x	x	x	x
Hoho marilla	Melitidae	A	41	6	192		x	x	x	x
Tanaidae spp.	Tanaidae	T	36	6	157		x	x	x	
Paraproto spinosa	Caprellidea	A	34	6	63		x			
Cymadusa spp.	Ampithoidae	A	33	6	86		x	x		
Podocerus sp.	Podoceridae	A	31	6	122		x	x	x	x
Plakarthrium australiensis	Plakarthridae	I	30	4	90	EB, EP	x	x		
Ampithoe geographe	Ampithoidae	A	28	6	95		x	x		
Gabophilas sp.	Philantidae	A	25	5	84	NP	x	x		
Ampithoe spp.	Ampithoidae	A	23	6	104		x	x	x	x
Haswellia emarginata	Sphaeromatidae	I	23	5	44	NP	x			
Cyproidea ornata	Cyproideidae	A	21	6	38		x			
Paradexamine frinsdorfii	Dexaminidae	A	15	3	44	NP, SI, WI	x			
Amphoroidea cf *angustata*	Sphaeromatidae	I	11	3	35	EB, EP, WI	x			
Eusiridae sp. A	Eusiridae	A	11	4	50	EP, NP	x			
No. of taxa in best selection model (i.e. total x)							16	10	6	5
ρ for 'next best' model, following exclusion of taxa in 'best selection' model (i.e. x)							0.476	0.598	0.765	0.826

Table 5. BVSTEP analyses displaying sub-sets of Nuyts macroalgal taxa comprising the best selection models at ρ = 0.95, 0.9, 0.85, 0.8 and 0.75. At ρ = 0.7, the 'next best selection' model constitutes a viable alternative (i.e. ρ = 0.798). Taxa ranked by frequency of occurrence among samples. Total biomass measured in g dry wt. P: Phaeophyta, R: Rhodophyta and C: Chlorophyta; *out of n = 57 samples; **out of n = 6 sites

Taxonomic name	Order	Phylum	Present in no. of samples*	sites**	Total biomass	Absent from sites	ρ 0.95	0.9	0.85	0.8	0.75
Cystophora monilifera	Fucales	P	21	6	485.2		x	x	x	x	x
Sargassum varians	Fucales	P	20	4	181	SI, NP	x	x	x	x	x
Scytothalia dorycarpa	Fucales	P	17	4	500	EB, EP	x	x	x	x	x
Sargassum lacerifolium	Fucales	P	15	5	104.6	FI	x	x	x	x	x
Plocamium dilatatum	Plocamiales	R	14	5	54.4	EB	x	x			
Ecklonia radiata	Laminariales	P	13	4	255.3	EB, EP	x	x	x	x	
Caulerpa flexilis	Caulerpales	C	12	5	25	NP	x				
Sargassum spinuligerum	Fucales	P	11	3	81.3	WI, SI, NP	x	x	x		
Sargassum sp. A	Fucales	P	10	5	62.6	EB	x	x			
Zonaria spiralis	Dictyotales	P	10	4	51.8	EB, NP	x				
Sargassum verruculosum	Fucales	P	9	3	58.8	FI, SI, NP	x				
No. of taxa in best selection model (i.e. total x)							11	8	6	5	4
ρ for 'next best' model, following exclusion of taxa in 'best selection' model (i.e. x)							0.279	0.382	0.473	0.500	0.578

DISCUSSION

The conclusion that aggregating macrofaunal assemblages to the family level does not significantly alter the outcome of the analyses concurs with many other studies which have examined the effect of taxonomic resolution on multivariate analyses (e.g. James et al. 1995, Marchant et al. 1995, Wright et al. 1995, Vanderklift et al. 1996, Olsgard et al. 1997, 1998, Chapman 1998, Hewlett 2000, Metzeling et al. 2002). Similarity matrices derived for faunal assemblages identified to genus and family in this study were highly correlated with similarity matrices at the species level (ρ > 0.85) and displayed similar multivariate patterns. However, faunal taxa amalgamated to the level of order conveyed less information at both the scale of individual samples (Fig. 2) and sites (Table 2, Fig. 6). Fine-scale spatial information such as that conveyed between samples may not be entirely necessary or in fact informative, depending on the scope of the study considered (e.g. spatial autocorrelation, Somerfield & Gage 2000). Nevertheless, this finding raises questions about the potential power and sensitivity of tests conducted at the order-level. For one data set, the aggregation of data to the order-level led to reduced separation of sites (Table 2), whereas ordinal data was sufficient to distinguish both habitats and sites among the Fleurieu faunal samples (Table 3). Anderson et al. (2005b) using a multi-scale hierarchical design, detected the greatest amount of variation in faunal assemblage structure at the smallest sampling scale (i.e. between individual kelp holdfasts) regardless of the taxonomic resolution used, however, the amount of variation explained at this scale diminished progressively beyond the family level.

Other studies have indicated that quite low levels of taxonomic resolution (i.e. order or phylum) were sufficient to detect changes in communities impacted by pollution (Smith & Simpson 1993, Somerfield & Clarke 1995, Wright et al. 1995, Stark et al. 2003). However, Olsgard et al. (1998) found that data sets aggregated to coarser taxonomic levels were less informative for environments free of pollution, when compared to samples collected along a clear disturbance gradient. This finding suggests that detection of community patterns in non-impacted sites (where a range of natural gradients predominate), is not necessarily achievable using very coarse levels of taxonomic classification (i.e. order and beyond). The analyses conducted for the Nuyts faunal data largely supported this conclusion (Table 2 and Fig. 6), while the results from the Fleurieu faunal data were more equivocal (Table 3).

This study departs from the above studies with regard to the conclusions reached for macroalgal assemblages. Aggregating algal biomass data above the species-level (to genus or family) distorted the correlation between rank inter-sample similarities to a greater extent than that observed for the faunal data (Fig. 2). The strength of the correlations between site exposure and macroalgal assemblage structure (Fig. 6) and the degree to which the sites could be separated in multidimensional space diminished progressively (Table 2), to the extent where order- and phylum-level identifications of algae explained very little of the pattern inherent at the species level. Genus- and family-level identifications, in this instance, clearly explained less information than the species data, particularly when contrasted with the faunal data. I am not aware of any other study that has examined the merits of

using lower taxonomic resolution when surveying macroalgal communities, despite the fact that the same difficulties and costs associated with processing and identifying diverse faunal samples apply. This is particularly true of southern Australia where algal diversity is exceptionally high (Phillips 2001) and the identification of some groups is often difficult (e.g. Rhodophytes). Successful identification of some species requires not only considerable taxonomic expertise, but also the presence of fertile reproductive structures. Instead, these difficulties have prompted a more functional approach to the ecological classification of macroalgal assemblages (e.g. functional groups, Steneck & Dethier 1994). However, the usefulness of these models has been criticised (Padilla & Allen 2000) and algal functional groups appear to act as poor proxies for species-level information among temperate reef communities (Phillips et al. 1997). It is therefore surprising that the application of higher-level taxonomic resolution to macroalgal survey work has not been more widely explored in locations where regional algal diversity is relatively high.

The loss of information, compared to the faunal data, conveyed by aggregating macroalgal species at taxonomic levels higher than species was related to the diversity and dominance of the fucoid algae amongst these samples (see BVSTEP analyses, Table 5). The order Fucales is richest in southern Australia (61 species in 15 genera: Womersley 1987) but nearly all taxa are subtidal in contrast to the largely intertidal Fucalean taxa found on northern hemisphere coasts. The canopy assemblages analysed in this study included 12 fucoid species within 3 genera; *Sargassum* (7 species), *Cystophora* (4 species) and *Scytothalia* (a single species *S. dorycarpa*). Fucoid species dominated 5 of the 6 locations sampled, and were co-dominant with the laminarian kelp *Ecklonia radiata* at the 6th site (see Hirst 2003 for further details). Consequently fucoid species dominated the taxa in the 'best selection' model (BVSTEP analysis; $\rho = 0.95$) and included 7 of the 11 taxa selected, 5 of which were *Sargassum* species (Table 5). Thus, when the assemblage data were aggregated at the genus-level, and subsequently the family-level, this fine detail was lost, particularly between sites. By comparison, this pattern was less apparent for the faunal assemblages where fewer higher taxa dominated the 'best selection' model (see Table 4). Whether this is a common phenomenon amongst macroalgal communities of southern Australia remains to be more rigorously tested using more spatially extensive data sets (e.g. Collings & Cheshire 1998, Wernberg et al. 2003).

There are a number of advantages to using coarser taxonomic resolution for surveying subtidal rocky reef communities other than the obvious savings in time and money, although such savings can be quite considerable. In a study of soft-bottom communities, Ferraro & Cole (1995) estimated that the costs of genus-, family-, order- and phylum-level identification were, respectively, 23, 50, 80 and 90% less than species-level identification for soft-sediment infaunal samples. Such cost-savings can be reallocated to greater sample replication and improved sampling design (e.g. additional control sites), hence giving greater statistical (detection) power. I am not aware of any equivalent information for epifaunal assemblages, although the savings are likely to be of a similar magnitude. In this study, specimens were initially sorted to the level of order but required further scrutiny for identification to family-level and beyond. Faunal identification at the species-, genus- and family-level often requires dissection of specimens and the use of appropriate taxonomic keys and literature; in the case of this and other studies, specimens were also sent to museum experts, further lengthening the process. Thus, the use of coarser levels of taxonomic resolution may also circumvent the need for species-level taxonomy or detailed taxonomic expertise, which may not be readily available in some parts of the world.

One other clear benefit of using a coarser taxonomic resolution is that comparisons between independently collected data sets are simpler (inter-sample comparisons). This is because of the difficulties associated with integrating species identifications across surveys. This is particularly problematic where there have been major taxonomic revisions of certain groups or where voucher collections have not been retained and the identity of specimens is uncertain, as is often the case for many historical data sets. For southern Australian temperate reef communities, this is likely to be more of a problem for the fauna, a large proportion of which remain undescribed, than the algae, which (excepting the Rhodophyta) have a largely settled taxonomy. Finally, due to the difficulties with consistently identifying specimens to species, the accuracy and hence certainty of specimen identifications generally increases with decreasing taxonomic resolution (Hewlett 2000).

Clearly, some information is lost when specimens are progressively identified to levels above species. However, the extent to which this information is important to the user needs to be assessed on a case-by-case basis (e.g. Ferraro & Cole 1995) and in line with the objectives of the study (see also Anderson et al. 2005b). One potential difficulty with using taxonomic identifications higher than species, in particular quite coarse levels of identification such as order or phylum, is that although lower taxonomic resolution may be sufficient to identify patterns in community structure, analyses conducted at this level may give us little clue regard-

ing the potential mechanisms behind such patterns. For example, in Hirst (2007) differences in faunal assemblage structure between canopy and understorey habitats were related to the distribution of functional-feeding groups between habitats. Functional feeding behaviour varied considerably within orders and was assigned using genus- and family-level information; thus, the use of coarser levels of taxonomy would have obscured the actual mechanism and the general applicability of conceptual models arising from such a finding.

This argument, however, can be presently overstated because fundamental ecological information is often lacking at the species-level as the vast majority of species (especially in the southern hemisphere) have never been studied. Species-level information will, however, still be required to identify species with potentially vulnerable distributions (i.e. those with limited or isolated populations and/or overall low abundance), detect and monitor the impact of introduced species (Wilson et al. 1998) and for biogeography (Thiel 2003). Species inventories will therefore remain an important, if more costly, component of studies that have either a conservation or biodiversity emphasis.

This study makes separate recommendations regarding the sufficiency of various levels of taxonomic resolution for describing change in (1) faunal and (2) algal communities associated with subtidal reef habitats in southern Australia. Among the faunal data sets, identifications to the family level were adequate to infer patterns in community structure and indeed data sets aggregated at the family- and species-level were highly correlated. Keys to families for many of the arthropod taxa are readily available (e.g. Lowry & Springthorpe 2001) and thus family-level identifications are attainable with only a modest level of expertise. Order-level identifications may also be sufficient in some instances, although the level of discrimination in this study was always lower than that apparent at the species-, genus- and family-level, and information at the fine spatial-scale (i.e. between samples) is clearly lost; this may lead to erroneous conclusions about the structure of assemblages in both space and time, particularly for more complex data sets. By comparison, aggregating macroalgal taxa to levels higher than species resulted in the loss of considerably more information to the point where, at very coarse levels of taxonomic identification (e.g. order and phylum), very little of the structure present at the species level was retained. Thus, it would seem that aggregating macroalgal data at levels higher than species might not be as an informative approach as it is for the fauna. This conclusion, however, is based on a single algal data set and requires more extensive testing before firmer recommendations can be made. These recommendations only apply to studies conducted at similar spatial scales (m to km) and may need to be reassessed at broader spatial scales (Anderson et al. 2005b). Overall, this study suggests quite fundamental differences in the way that faunal and algal communities assemble at the species level among subtidal reef communities in southern Australia.

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