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Influence of taxonomic resolution and morphological functional groups in multivariate analyses of macroalgal assemblages

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This paper examines how the use of various taxonomic levels and morphological functional groups influences the interpretation of multivariate analyses when comparing macroalgal assemblages in different regions in the Northeast Pacific. We found that for intertidal assemblages, within-site variation was high at the species level and regions only became discernable from the genus level to the order level. Above order level, regions were less well distinguished. Differentiating assemblages at the genus level were similar to results from functional group analyses. This implies that various levels and morphological functional groups can be used to distinguish intertidal assemblages among regions. Intertidal strata differences could be discerned at all taxonomic levels and using functional groups. In contrast to the intertidal, only a few regions were significantly different for subtidal assemblages, independent of taxonomic resolution used. Functional grouping in subtidal assemblages yielded the same resolution as taxonomic levels. Conversely to the intertidal assemblages, strata differences in the subtidal were found at the species and genus levels and with functional groups but not at the family and higher levels. Overall, these results demonstrate differences in regional and strata comparisons in intertidal and subtidal assemblage analyses and that typically species-level analyses are not required.

Key Words: Macroalgae, Morphological functional group, Rocky intertidal, Subtidal, Taxonomic resolution

INTRODUCTION

Many studies comparing biological communities, either for similarities/differences or for examining impacts of environmental perturbations, have focused their attention on species-level identifications. Although species-level identification usually provides greater resolution than higher taxonomic level identification (*sensu* taxonomic sufficiency, Ellis 1985), it also takes considerable time and is associated with high costs. For example, Ferraro and Cole (1995) observed species-level identification of soft-bottom communities to be twice the monetary cost of family-level identification and almost five times that of order-level identification. Along with time and costs, species-level identification requires more taxonomic expertise and may yield more error in identifications, which may bias the interpretation of the results. Recently, several published papers from many different ecosystems have examined the practicality of using various taxonomic levels to do community analyses on invertebrates (e.g. Gray *et al.* 1990; Vanderklift *et al.* 1996; Bowman & Bailey 1997; Olsgard *et al.* 1997; Thompson & Townsend 2002; Dauvin *et al.* 2003; Terlizzi *et al.* 2003; Anderson *et al.* 2005). For example, it was found that family-level identifications were adequate to infer patterns in community structure for arthropods and that aggregating data at the family and species levels were highly correlated (Hirst 2006). Similarly for polychaetes, family richness was significantly correlated to total species richness (Olsgard *et al.* 2004). It should be noted, however, that there is no general agreement that there is justification for the use of higher taxonomic levels for biodiversity assessments (Bertrand *et al.* 2006). It has been suggested that the use of higher taxa is founded on misconceptions about Linnaean classification properties in that rank allocations in current classification systems represent a heterogeneous mixture of various historical and modern opinions.

As opposed to taxonomic diversity, the use of invertebrate functional groupings or guilds (such as morphology, feeding, motility, and reproductive modes) in community analyses has also become common. For example, chiton radula morphological functional groups have been used to examine grazing effects on macroalgal community structure (Steneck & Watling 1982). Also, feeding functional groups have been used to relate community changes with water chemistry (Maurer & Leathem 1981; Holte *et al.* 2005; Coyle *et al.* 2007). Functional analyses of motility also have been examined in various soft-sediment habitats (Pearson 2001). Functional groups have, however, not always been found to be useful. In a study that attempted to correlate polychaete feeding functional groups with water depth, median phi size, and percentage silt-clay of the sediment, it was found that the feeding groups were defined too broadly to be useful for estuarine systems (Dauer 1984).

For many practical and ecological reasons, it is important to know what impact the level of taxonomic resolution or the use of functional groups instead of taxonomic identification has on the outcome of community analyses. Although this question has been discussed in the literature for several invertebrate groups, information regarding macroalgal taxonomic resolution as well as the use of functional groups is far scarcer.

Although one study did find that aggregating macroalgal taxa to higher than species levels resulted in a substantial

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loss of information, that study only examined one site and one subtidal depth and recommended that this analysis be conducted on a larger spatial scale (Hirst 2006). Morphological functional-group classifications (Littler & Littler 1980) have been widely used to address physiological questions (e.g. Littler & Arnold 1982; Johansson & Snoeijs 2002), to investigate the impact of herbivore grazing (e.g. Dethier 1981; Steneck & Watling 1982; Iken 1999) and also are becoming more common in ecological studies of macroalgal communities (Steneck & Dethier 1994). For example, a study that examined algal recruitment found that colonization patterns were not as clear at the species level when compared with the morphological functional-group level, implying that knowledge on the ecology of individual species will increase our predictive power in describing a community (Benedetti-Cecchi 2000). The purpose of this paper is to analyze the effect of using (1) different levels of taxonomic aggregation, and (2) morphological groups in the analyses of similarity patterns of intertidal and subtidal macroalgal assemblages in the North Pacific. The use of functional groups was explored because little is known about if and how taxonomic resolution relates to macroalgal functional groups.

MATERIAL AND METHODS

Macroalgal assemblages were sampled in three regions in the Gulf of Alaska, separated by approximately 200 km in summer 2003 and at one site in the British Columbia region in summer 2006. In each region in the Gulf of Alaska, three sites separated by at least 1 km were sampled. In the Kodiak Island region, sites were Old Harbor, Alitak, and Uyak Bay. In the Kachemak Bay region, sites were Elephant and Cohen islands and Outside Beach. In the Prince William Sound region, sites were Montague, Knight, and Green islands. Bath Island was the site sampled in the Strait of Georgia, British Columbia region. All together, these sites spanned a linear distance of approximately 4500 km (longitudinally from 123°40′W to 154°15′W and latitudinally from 49°04′N to 60°39′N). All sites were chosen qualitatively on the basis of similar exposure to hydrodynamic forces, verticality, and substrate type.

Macroalgal biomass was estimated at the study sites using standardized protocols developed for the Natural Geography In Shore Areas (NaGISA) program within the Census of Marine Life (Rigby *et al.* 2007). NaGISA uses a stratified random sampling design in which five replicate random samples are collected at each site along a 30-m transect in each of the high, mid-, and low intertidal strata, and from 1-, 5-, 10-, and 15-m-deep subtidal strata (relative to mean lower low water). Although a sample size of five is relatively small, NaGISA protocols are widely used throughout the world and as such, the analyses that we perform here have wide application to existing and developing data sets to be used in monitoring and as a baseline for hypothesis testing. Intertidal strata were determined and easily distinguished on the basis of prevailing biobands (i.e. high was dominated by *Fucus* bands, mid by large red algal bands, and low by large red and brown algal bands). At three sites (Kachemak Bay's Outside Beach, Kodiak Island's Old Harbor and British Columbia's Bath Island), the 15-m stratum was not sampled because the substrate was 100% sand. For each replicate all macroalgae were scraped from within a 50- × 50-cm quadrat. Algae were sorted to the species level and their wet weights determined using an analytical scale at 0.1 g precision. Thin encrusting red, brown, and coralline algae were excluded from this study because they could not be completely cleared from the substrate.

Taxonomic affinities (higher taxonomic levels) were classified according to the Algaebase web site (www.algaebase.org). Biomass data were analyzed at different taxonomic levels using the software package Primer (v6, Plymouth Marine Laboratories, Clarke & Warwick 2001). Within Primer, biomass data were log(x+1) transformed, and nonmetric multidimensional scaling (nMDS on the basis of Bray–Curtis similarity matrices) and analysis of similarities (ANOSIMs) were applied to various taxonomic levels. For the regional comparison a two-way nested ANOSIM was applied to the raw data and for the stratum comparison, a two-way crossed ANOSIM was applied to mean data per stratum (across all sites per region). It should be noted that ANOSIM does not enable tests of interactions among strata and the two nested spatial scales (sites within region) so our conclusions about the effect of changing taxonomic resolution are limited to a test of the main effect of stratum, but these effects do not necessarily reflect what would happen for interactions. Taxonomic levels examined included the following: species, genus, family, order, class, and division. Morphological functional groups included the following: nonbranching filament, finely branched filament, coarsely branched filament, monostromatic or distromatic sheet, blade, leathery blade, branched blade, canopy kelp, thick crust, pustule, peltate blade, sac, and upright corallines (modeled after Littler & Littler 1980). Intertidal (high, mid-, low and 1 m) and subtidal (5, 10, and 15 m) assemblages were analyzed separately as these strata represent different communities (Konar & Iken unpublished data).

RESULTS AND DISCUSSION

Regional comparison of community assemblages using various taxonomic levels and morphological functional groups differed for intertidal and subtidal assemblages. For intertidal assemblages, nMDS showed that regions separated the most clearly from the genus level to the order level (Fig. 1). At the species level, it appears there may be too much variation within a site to be able to distinguish regions. At the class and division level, Prince William Sound and Kachemak Bay were no longer distinguishable (Table 1). In the intertidal analysis, the morphological functional group approach was useful for distinguishing assemblages, and yielded results similar to taxonomic resolution at the genus level (Fig. 1 and Table 1).

Unlike intertidal assemblages, subtidal analysis demonstrated that regions were equally discernable at all taxonomic levels and using the morphological functional

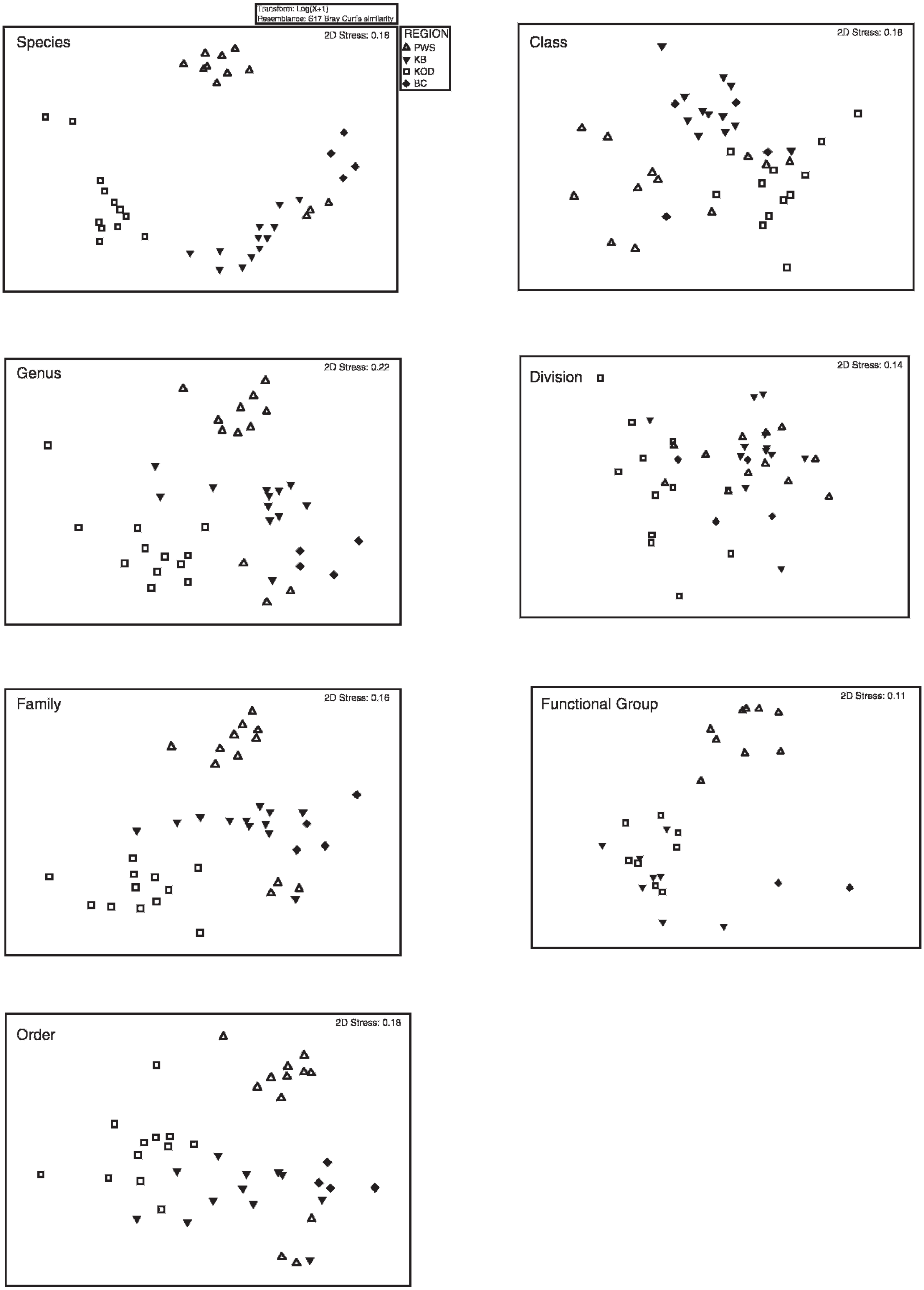
Transform: Log(X+1)
Resemblance: S17 Bray Curtis similarity
REGION
PWS
KB
KOD
BC
Species
2D Stress: 0.18
Class
2D Stress: 0.18
Genus
2D Stress: 0.22
Division
2D Stress: 0.14
Family
2D Stress: 0.16
Functional Group
2D Stress: 0.11
Order
2D Stress: 0.18

Table 1. Two-way nested ANOSIM for differences among regions in intertidal macroalgal assemblages and two-way crossed ANOSIM for differences among depth strata for intertidal macroalgal assemblages.

		Differences among regions					Differences among strata		
		Global *R* and sample statistic	Pairwise			*P*-value	Sample statistic	*P*-value	
Resolution	# taxa	Region	Regions	R Statistic		Region	Strata	Region	
Species	184	0.605	PWS,[1] KB	1	*	0.1	0.37	0.03	*
		0.1	PWS, KOD	0.259		0.2			
			PWS, BC	1	*	0.25			
			KB, KOD	0.37		0.1			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Genus	91	0.679	PWS, KB	0.926	*	0.1	0.49	0.009	*
		0.1	PWS, KOD	0.259		0.1			
			PWS, BC	1	*	0.25			
			KB, KOD	0.593	*	0.1			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Family	35	0.716	PWS, KB	1	*	0.1	0.66	0.004	*
		0.3	PWS, KOD	0.333		0.1			
			PWS, BC	1	*	0.25			
			KB, KOD	0.704	*	0.1			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Order	20	0.63	PWS, KB	0.926	*	0.1	0.64	0.004	*
		0.1	PWS, KOD	0.259		0.2			
			PWS, BC	1	*	0.25			
			KB, KOD	0.593	*	0.1			
			KB, BC	1	*	0.05			
			KOD, BC	0.778	*	0.25			
Class	6	0.543	PWS, KB	0.148		0.1	0.73	0.001	*
		0.2	PWS, KOD	0.37		0.1			
			PWS, BC	1	*	0.25			
			KB, KOD	0.667	*	0.1			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.1			
Division	3	0.543	PWS, KB	0.259		0.1	0.59	0.01	*
		0.1	PWS, KOD	0.37		0.1			
			PWS, BC	1	*	0.25			
			KB, KOD	0.63	*	0.1			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Functional Group	14	0.679	PWS, KB	0.889	*	0.1	0.49	0.03	*
		0.1	PWS, KOD	0.37		0.2			
			PWS, BC	1	*	0.25			
			KB, KOD	0.741	*	0.1			
			KB, BC	1	*	0.25			
			KOD, BC	0.778	*	0.25			

[1] PWS, Prince William Sound; KB, Kachemak Bay; KOD, Kodiak; BC, British Columbia.
* Refers to comparisons that are significantly different.

group approach (Fig. 2 and Table 2). At all levels, assemblages within the Gulf of Alaska could not be separated; whereas, at all levels, British Columbia was always separated from the Gulf of Alaska regions (Table 2).

Examining the assemblages for differences among depth strata also resulted in different interpretations for the intertidal and subtidal. For the intertidal assemblages, differences among strata were found at all taxonomic levels and with the functional groups (Table 1). For the subtidal assemblages, differences among strata occurred at the species and genus level, and also using the functional groups (Table 2). In contrast, family-, order-, class-, and division-level analyses did not demonstrate any subtidal stratum differences. It appears that for intertidal algal assemblages, all levels give good resolution when comparing strata, but for the subtidal, lower taxon levels (i.e., species or genus) or morphological functional groups have to be used for stratum resolution. This discrepancy could be caused by the biomass in subtidal algal assemblages being

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Fig. 1. nMDS of intertidal macroalgal communities at various resolution levels, including species, genus, family, order, class, division, and morphological functional group. PWS = Prince William Sound, KB = Kachemak Bay, KOD = Kodiak, BC = British Columbia.

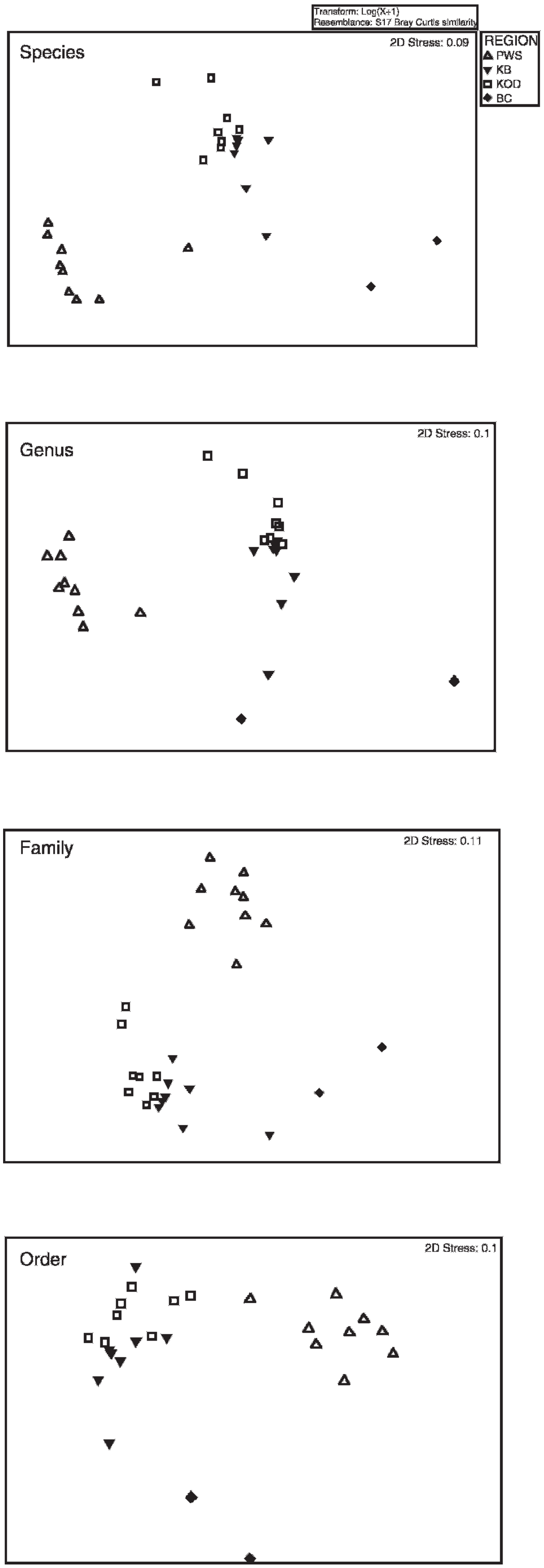
Transform: Log(X+1)
Resemblance: S17 Bray Curtis similarity
REGION
PWS
KB
KOD
BC
Species
2D Stress: 0.09
Class
2D Stress: 0.14
Genus
2D Stress: 0.1
Division
2D Stress: 0.11
Family
2D Stress: 0.11
Functional Group
2D Stress: 0.11
Order
2D Stress: 0.1

Table 2. Two-way nested ANOSIM for differences among regions in subtidal macroalgal assemblages and two-way crossed ANOSIM for differences among depth strata for subtidal macroalgal assemblages.

		Differences among regions					Differences among strata		
		Global *R* and sample statistic	Pairwise				Sample statistic	*P*-value	
Resolution	# taxa	Region	Regions	*R*		Signif. level %	Strata	Region	
Species	145	0.321	PWS,[1] KB	0.111		0.2	1	0.03	*
		1	PWS, KOD	0.296		0.2			
			PWS, BC	1	*	0.25			
			KB, KOD	0.074		0.4			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Genus	86	0.346	PWS, KB	0.074		0.3	1	0.03	*
		0.5	PWS, KOD	0.37		0.1			
			PWS, BC	1	*	0.25			
			KB, KOD	0.074		0.3			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Family	36	0.364	PWS, KB	0.037		0.5	0.67	0.19	
		0.3	PWS, KOD	0.37		0.1			
			PWS, BC	1	*	0.25			
			KB, KOD	0.037		0.3			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Order	22	0.321	PWS, KB	0.222		0.2	0.67	0.19	
		1.3	PWS, KOD	0.037		0.5			
			PWS, BC	1	*	0.25			
			KB, KOD	0		0.5			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Class	7	0.222	PWS, KB	0.074		0.8	0.17	0.36	
		7.2	PWS, KOD	0.111		0.7			
			PWS, BC	1	*	0.25			
			KB, KOD	0.148		1			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Division	3	0.216	PWS, KB	0.074		0.7	0.67	0.18	
		8.5	PWS, KOD	0.074		0.6			
			PWS, BC	1	*	0.25			
			KB, KOD	0.074		0.8			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			
Functional group	13	0.302	PWS, KB	0.037		0.3	1	0.03	*
		1.7	PWS, KOD	0.074		0.5			
			PWS, BC	1	*	0.25			
			KB, KOD	0.074		0.4			
			KB, BC	1	*	0.25			
			KOD, BC	1	*	0.25			

[1] PWS, Prince William Sound; KB, Kachemak Bay; KOD, Kodiak; BC, British Columbia.
* Refers to comparisons that are significantly different.

dominated by few kelp species (Laminariales); whereas, there is more species diversity and less individual taxon biomass in the intertidal.

Higher taxonomic levels or functional groups may be warranted for some macroalgal assemblage analyses, but the type of question asked also will dictate the level of taxonomic resolution needed and whether functional groups can be used. Obviously, if a monitoring program is being established to find invasive species, then the species level must be used. Similarly, it has been shown that species-level identification is the best when determining biodiversity hot spots and areas of highest conservation priority (Fjeldså 2000; LaFerla *et al.* 2002). The results of this study imply that for macroalgal assemblages, higher taxonomic levels or functional groups might be appropriate for certain questions and comparisons. Particularly, analyses on higher taxon levels have been shown to help eliminate environmental ''noise'' caused by natural variation, which is often a confounding factor in species-level analyses (Warwick 1988a, b) and is probably the reason why Kachemak Bay and Kodiak Island intertidal assemblages were not discernable at the species level. If impacts

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Fig. 2. nMDS of subtidal macroalgal communities at various resolution levels, including species, genus, family, order, class, division, and morphological functional group. PWS = Prince William Sound, KB = Kachemak Bay, KOD = Kodiak, BC = British Columbia.

due to a stressor are to be determined, then either a higher taxonomic level or functional group may be applicable (Warwick 1988a, b; Stark *et al.* 2003; Thompson *et al.* 2003); although, species-specific responses to environmental stress may differ even if species belong to the same higher taxonomic or functional group. Also, higher taxonomic levels will likely produce robust and repeatable answers to questions concerning the detection of food-web properties (Hall & Raffaelli 1991) and perhaps the biodiversity conservation to establish reserve networks (Balmford *et al.* 1996, 2000). Our results show that analysis on higher taxonomic levels may be particularly appropriate for subtidal assemblages, as regional differences did not change with taxonomic level. However, our results also show that care must be taken in distinguishing between intertidal and subtidal macroalgal assemblages as their sensitivity differs toward various taxonomic levels and functional groupings.

We have shown that species-level identification may not always be needed when analyzing macroalgal assemblages. In general for macroalgal assemblages, when species identity (e.g. for biodiversity, conservation, introduced species) is important, then species-level identification will be needed; however, for community-wide impacts, where species identity is not important, then higher identification levels may be sufficient to reliably discern assemblage similarities/differences. In fact, species-level identification may introduce more variation, making it difficult to find general similarities within regions. Higher taxa analyses usually are cheaper, more efficient, require less taxonomic expertise, and remove possible errors in identification. Although our observations were only from one sampling period and only from a limited number of sites and regions within the North Pacific, higher taxonomic-level analyses were mostly able to distinguish these regions, particularly in the intertidal. It would be worthwhile to expand these analyses to multiple spatial scales tens of kilometers to thousands of kilometers) to determine the generality of our results.

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