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Detecting benthic responses to human-induced change: effectiveness of alternate taxonomic classification and indices

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ABSTRACT: Our understanding of the ecological consequences of human activities may change based on our choice of taxonomic classifications used to observe ecological patterns. We tested the effects of water pollution (nutrient enrichment) and over-harvesting (loss of grazers) on several measures of algal abundance and diversity. These measures included the percentage cover and biomass of individual species and morphological groups, as well as indices that aggregate the response of species, i.e. species diversity (Shannon index) and the less commonly used Abundance-Biomass Comparison (ABC) curves and phylogenetic diversity. Together, all observed responses suggested that nutrients had the largest effect, whether positive (e.g. biomass of sediment-trapping algae), negative (e.g. phylogenetic diversity), or exacerbated by loss of grazers. The interaction between nutrients and grazers was only detected by 2 indices that relied on phylogenetic classifications (ABC curves and phylogenetic diversity). The more traditional aggregate index (Shannon index) did not detect the effect of either nutrients or grazers. Non-indices (i.e. biomass of morphological groups) were sensitive only to the experimental influence of nutrients, whereas observations of individual species alone could not detect the effects of any treatments. These differences highlight the importance of classification (e.g. morphology versus species) and indices (e.g. Shannon index versus ABC curves and phylogenetic diversity) in their potential to predetermine our perception of ecological change and predictions of future environments.

KEY WORDS: Environmental change · Macroalgae · Taxonomic classification · Diversity index

INTRODUCTION

The need to predict future environments as a consequence of human activity in part requires understanding contemporary responses (e.g. Vitousek et al. 1997, Jackson et al. 2001). In benthic marine ecology, such understanding requires the ability to detect changes in composition and abundance of sessile assemblages. While such research has become increasingly intense, there has been less consideration of the potential for benthic responses to vary as a consequence of classifications (e.g. species, morphology, function) and indices (species richness, Shannon index, phylogenetic diversity) used to measure response.

There is a history of concern over the choices of variables used to observe patterns and quantify changes in macroalgal assemblages (e.g. Padilla & Allen 2000). While the loss of species can alter entire systems (e.g. Hooper et al. 2005), the detection of change through the use of broader taxonomic classifications (i.e. morphological group hypothesis) can be informative (Tilman 2001) or potentially more predictive (Keddy 1990, Hay 1994) because of the fundamental nature of change brought by human-induced disturbance (Jackson et al. 2001). Species-level approaches to detecting change have been questioned on the basis of cost (i.e. labour-intensive and taxonomic expertise required) and ecological relevance (e.g. species-specific changes

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may have little overriding affect on whole assemblages; Littler & Littler 1980, Steneck & Dethier 1994). While the morphological/functional group hypothesis may provide broad insight into community structure, it too has its disadvantages. One of the fundamental problems with the use of these groupings is their lack of sensitivity to detecting change, particularly in regard to algal assemblages, which may be relatively insensitive to environmental gradients, compared to species-specific approaches (Phillips et al. 1997, Padilla & Allen 2000).

Ecologists are faced with decisions about not only taxonomic classifications, but also which metric to use to assess the response on assemblages, i.e. uncomplicated summaries (percentage cover, biomass, number of species) versus indices (Abundance-Biomass Comparison [ABC] curves, Shannon index, phylogenetic diversity). Researchers often feel compelled to reduce complex ecological data into a single index so that their results can be more readily interpreted by managers and policy makers (Pardal et al. 2004). 'Biodiversity' is commonly used to assess environmental stress, disturbance and degradation within ecological systems, and the use of diversity indices enables distilling the information contained in a species abundance distribution into a single comparable statistic. For example, measures of phylogenetic diversity of species provide estimates of richness in terms of the number of distantly related species present in an assemblage. It has been hypothesised that lower values of diversity (i.e. closer phylogenetic relatedness of species) are indicative of assemblages subjected to anthropogenic disturbance (Clarke & Warwick 2001). However, the choice of index is also difficult in that some of the more traditionally accepted indices (e.g. Shannon index of diversity) are highly sensitive to sampling design and therefore may be more contingent on levels of sampling effort than levels of anthropogenic disturbance (Magurran 2004).

In the marine environment, human activities alter the composition and abundance of benthic organisms by mediating their rates of productivity (e.g. water pollution) and consumption (e.g. modification of herbivore numbers). Such activities may have larger consequences for the recovery (an issue of resilience) than persistence (an issue of resistance) of systems dominated by habitat-forming organisms with naturally high rates of turnover (e.g. natural mortality of corals and kelps; Hughes & Jackson 1985, Hatcher et al. 1987). It maybe useful, therefore, to understand how human activities affect developing assemblages, particularly those assemblages that influence the recovery of habitat-forming organisms.

On rocky temperate coasts, the predominant habitats (i.e. macroalgae) represent naturally disturbed systems (Witman & Dayton 2001) that are susceptible to human-mediated changes in productivity and consumption. For example, human-derived subsidies of resources (e.g. nutrients) appear to facilitate the persistence of opportunistic species of algae, a phenomenon that corresponds to the extensive covers of low-lying and sediment-trapping algae in the receiving waters of urbanised and agricultural watersheds (Connell 2007). Consumption can be affected by the fishing and subsequent population declines of herbivores (Andrew et al. 2002) and fishing of apex predators that trigger population increases of herbivores (Estes et al. 1998, Steneck et al. 2002). The need to understand these synergies motivates a substantial proportion of contemporary research, and there is an ongoing and basic requirement to understand how our classifications (e.g. morphology versus species) and indices (e.g. Shannon index versus ABC curves and phylogenetic diversity) may predetermine our perception of ecological change and forecasts of future environments.

In this study we compared the capacity of (1) classifications of morphological groups and species (biomass and percentage cover) and (2) 3 indices of diversity (ABC curves, Shannon index, phylogenetic diversity) to detect the effects of treatments on new space (i.e. perception of ecological change). We used a small-scale manipulative experiment of similar design (number of factors, levels and replications) to most experimental studies that test the effects of change. Experimental studies are unavoidably constrained by logistics. A review of 65 experimental studies published since 1993 (n = 14 aquatic journals), revealed that 83% of the studies covered limited spatial extent and tested community responses to only 1 or 2 factors (i.e. 2 stressors in combination). More than 50% of these studies included no more than 2 levels per factor and 5 replicates per level (Appendix 1). Given this practice, we designed a small-scale experiment (2 factors, each with 2 levels, n = 5) to test the sensitivity of alternate classifications and indices of benthic assemblage responses to pollution (water quality) and harvesting (loss of herbivores). Specifically, we tested the independent and combined effects of nutrient enhancement and grazer loss on erect macroalgal assemblages in a system where we reasonably expected a response to these perturbations (e.g. Russell & Connell 2005).

MATERIALS AND METHODS

Study site and experimental design. The experiment was done at Fishery Beach, Cape Jervis, South Australia (35° 35′ S, 138° 05′ E), a small southeast facing cove (~250 m across), with a reef extending 100 m perpendicular to the shore. The 125 d experiment took

place during the austral summer from November 2005 to March 2006. Experimental reefs (n = 20) were constructed from 60 × 60 cm metal frames on a double concrete base (60 × 60 cm) set on sand (Russell & Connell 2005) at approximately 4 m depth. The upper concrete base was 20 cm above the lower base and provided a platform for boulders collected from the natural reef. This design has been successfully used to exclude and test the effects of molluscan grazers and enhanced nutrients (Russell & Connell 2005).

The interactive effect of nutrients (ambient versus elevated) and grazing pressure (present versus absent) on algal assemblages was tested using a fixed, orthogonal design (n = 5 reefs per treatment). Fibro-cement settlement plates (15 × 15 cm) were prepared as either nutrient enhanced (n = 10) or ambient (n = 10). Nutrients were supplied as 2 × 200 g nylon mesh bags of Osmocote Plus® slow release fertiliser (6 mo release: 15, 5, 10 N-P-K) secured to opposite sides of plates. This configuration does not alter water flow, light, or sedimentation, or increase surface for settlement by algae on the upper side of the plate. Previous work has shown no detectable artefact (on algae abundance) between plates with or without the addition of control nutrient bags (Gorgula & Connell 2004). This method of nutrient enrichment of the water column is also the most effective for benthic environments (Worm et al. 2000). Nitrate concentrations were elevated from ambient (0.007 ± 0.002 mg l^{-1}) to 1.446 ± 0.291 mg l^{-1} across the experimental reefs in March. All plates were attached to boulders (n = 1 plate per experimental reef). Molluscan grazers were removed from natural reefs and placed on half of the experimental reefs (n = 10) at their natural densities, while the remaining reefs (n = 10) contained no molluscan grazers. Previous manipulations of herbivory using this technique show that translocated grazers continue to feed, as evidenced by the presence of grazing scars (Russell & Connell 2005).

Experimental reefs were regularly maintained (at intervals of approximately 14 to 28 d), so that nutrient bags were replaced and grazer densities replenished. After 125 d, settlement plates were placed in individual zip-lock bags with 4% buffered formalin (taking care not to dislodge any naturally settled sediment), and transported to the laboratory in black plastic drums, to prevent photodegradation of algae. In the laboratory, each plate was removed and the trapped sediment rinsed and oven-dried to a constant weight (70°C for 48 h) and analysed with a 2-factor analysis of variance (ANOVA) for differences in sediment weight between treatments.

Classification of morphological groups and species in experimental assemblages. The percentage cover and biomass (g dry weight) of each morphological group and species of algae was obtained after each plate was photographed and examined under a dissecting microscope (10×). Only the middle 12 × 12 cm of each plate was sampled to avoid edge effects. Percentage cover was estimated under a 12 × 12 cm grid containing 25 regularly spaced points under which each individual alga was removed. Precision and accuracy of estimating cover of broad taxonomic groups are not substantially affected by intensity and spacing of sampling (Drummond & Connell 2005). Analysis of species diversity involved sampling the entire centre (12 × 12 cm) of the 15 × 15 cm plate for the presence of all species (i.e. common and rare or cryptic species). Algal specimens were preserved in 4% formalin and stored.

All specimens removed were classified into morphological groupings according to the schemes proposed by Steneck & Dethier (1994) of (1) filamentous algae, (2) foliose, (3) corticated, terete (cylindrical and branching), (4) canopy forming and (5) articulated coralline algae. Individual algae sampled using the point-intercept method were digitally photographed, dried to constant weight, and identified as close as possible to species level. Voucher specimens of each species were sectioned, stained, and pressed, and taxonomic nomenclature followed Womersley (1984, 1987, 1994, 1996, 1998, 2003). The remaining assemblages on settlement plates were scraped, separated into appropriate species and morphological groupings, and dried and weighed.

Comparison of simple analysis measures (percentage cover and biomass) and indices. Multivariate analysis (PERMANOVA), using Bray-Curtis dissimilarity of fourth root transformed data, tested for differences in abundance (percent cover and biomass) of algal assemblages (morphological groups and individual species) due to treatments. Percentage of similarity analysis (SIMPER) was used to determine the morphological groups and species that contributed greatest to dissimilarity in biomass between treatments (Clarke 1993).

Two-factor ANOVAs and Student-Newman-Keuls (SNK) tests were used to test for differences in abundance for each morphological group, common species (occurring in >5% of samples) and diversity across treatments according to Underwood (1997). Data were analysed both with and without transformation to understand any effects of transformation and to meet assumptions of homogeneity of variance (Cochran's *C*-test). Importantly, there was no effect of transformation in detection of responses, and all transformations of data produced homogeneous variance where necessary. The variance component (σ^2) was calculated (Graham & Edwards 2001) to assess which factor, or combination of factors, primarily contributed to expan-

sive covers (percentage cover and dry weight) of each morphological group and species, and phylogenetic diversity of treatments.

Individual species sampled for each treatment (within 12 × 12 cm centre) were ranked in descending order in terms of abundance (number of individuals within samples) and biomass (dry weight), and each measure was converted to cumulative percent (as a proportion of total abundance/biomass on each plate). Cumulative measures of abundance for each treatment were graphically represented using ABC curves (cumulative abundance and biomass versus log species rank), and while currently used for infaunal polychaetes, we tested their applicability for use as an indication of short-term pollution in algal assemblages.

All taxa sampled were used for analysis of diversity between treatments using 2 diversity indices. As the Shannon index is calculated using the proportion of individuals from a certain species, abundance data (i.e. number of individuals within samples) was used. Presence/absence of individual species was used to calculate a measure of phylogenetic diversity, variation in taxonomic distinctness (VarTD), using PRIMER 5 software. Variation in taxonomic distinctness (hereafter phylogenetic diversity) measures differences in taxonomic structure between assemblages. A greater VarTD value indicates greater representation of genera (i.e. greater diversity). VarTD measures the evenness of phylogenetic relationships between taxa of an assemblage, whereas Shannon index (more commonly used as a measure of diversity) includes both the evenness and richness of species in an assemblage. For VarTD calculations, the longest path length (between phyla) was set to 100, and step lengths between taxonomic levels were assigned a weight of 6 to 1 (species, genus, family, order, class, phylum, respectively; Clarke & Warwick 1999). Differences in diversity (Shannon and VarTD) among treatments were analysed using a 2-factor ANOVA and SNK tests.

RESULTS

Morphological group and species composition

In total, 39 species were recorded across all treatments, and were unevenly distributed across the 5 defined morphological groups. Dominant morphological groups were corticated, terete algae (41% of all species) and filamentous algae (31%). Foliose algae represented 18% of the total species, with canopy-forming algae and articulated corallines being the most species-poor groups (5% of total species).

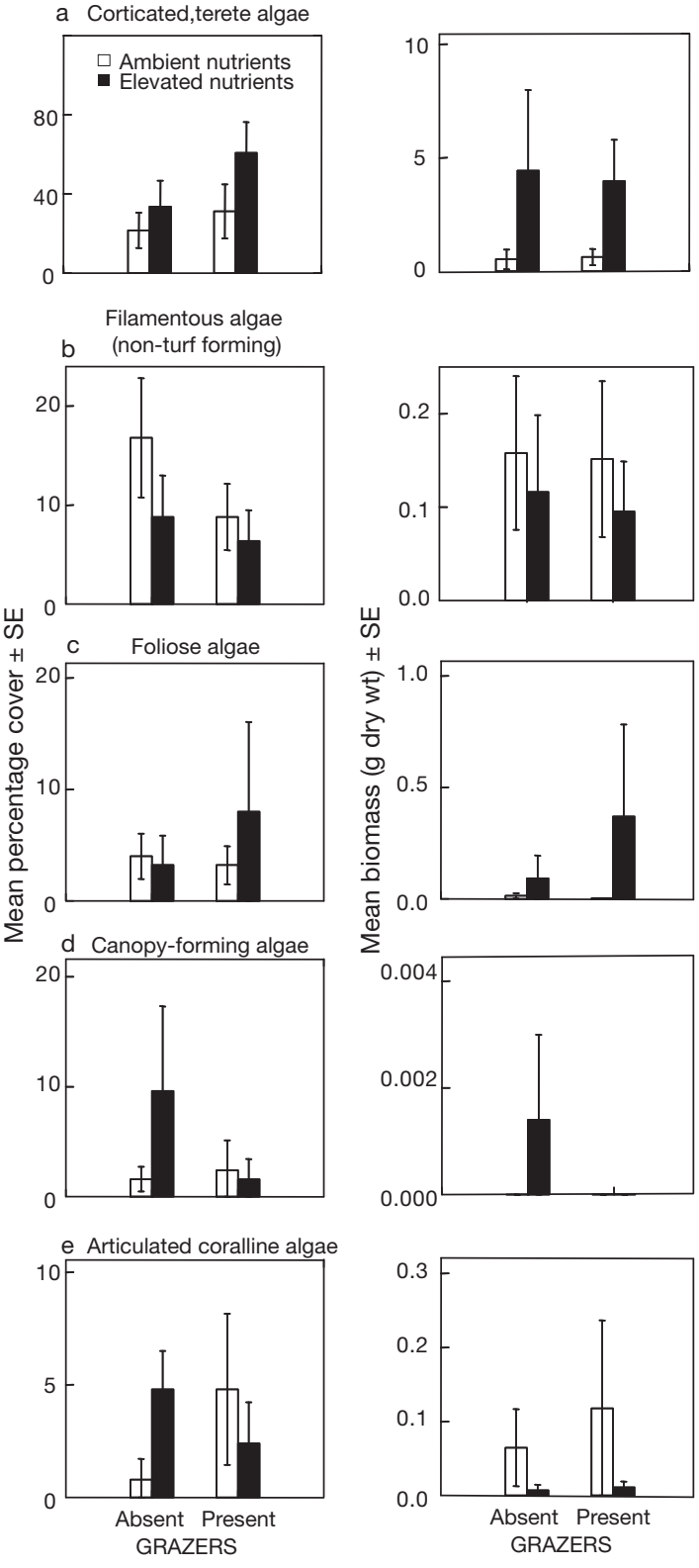

Fig. 1. Percentage cover (left) and biomass (right) (mean ± SE, n = 5) of morphological groups of algae exposed to elevated and ambient nutrient concentrations, both with grazers present and absent

Comparison of classification (morphology versus species) with simple measures

Morphological groups

Biomass of corticated, terete algae increased with elevated nutrient concentration (SNK: elevated nutrients [1.26 ± 0.28 g dry wt] > ambient [0.364 ± 0.13 g dry wt]; Fig. 1, Table 1), with nutrients accounting for the majority of the variation in biomass (σ^2 = 2.52, Table 1). No other morphological groups showed this significant response of biomass increase to treatments; however, the variance component of each factor shows that, with the exception of filamentous algae, nutrients has a larger influence than grazers (σ^2, Table 1).

Biomass of morphological groups was the only measure of assemblage structure sensitive enough to detect a response to perturbation. Elevated nutrients resulted in significant change in biomass (Table 2). The average dissimilarity between nutrient treatments (ambient versus enhanced) was 61.9% (SIMPER analysis), where corticated, terete algae contributed almost 67% of this dissimilarity (Table 3). Together, corticated, terete algae and filamentous algae explained a total of 82% between treatments, while biomass response of foliose and articulated coralline algae to nutrients contributed less than 10%. The biomass of sediment trapped within algae differed among treatments (ANOVA: $F_{1,16}$ = 14.74, p < 0.001; SNK tests: elevated nutrients [61.17 ± 9.28 g] > ambient nutrients [23.24 ± 3.70 g]) and were primarily associated with corticated, terete algae and filamentous algae (B. K. Roberts pers. obs.).

Species

Of the 39 species identified, only 2 occurred in >5% of samples. Neither percentage cover, nor biomass (dry weight) showed a significant relationship with either nutrient enrichment or removal of grazers for *Polysiphonia decipiens* (Fig. 2a) or *Doxydasya* sp. (Fig. 2b,

Table 1. Results of 2-factor ANOVA of cover and biomass (g dry wt) of morphological groups of algae among treatments of grazing intensity (ambient vs. reduced) and nutrient concentration (ambient vs. elevated). The variance component (σ^2) was calculated on untransformed data (Graham & Edwards 2001); **bold**: p < 0.05. Arcsine and ln (x + 1) transformations were used to meet assumption of homogeneity of variance for percentage cover and biomass data, respectively (Cochran's *C*-test)

Source	df	Cover (%)			Biomass (g)		
		MS	*F*	σ^2	MS	*F*	σ^2
Corticated, terete algae							
Grazers	1	878.320	2.710	51.94	0.070	0.120	0
Nutrients	1	1155.540	3.560	75.46	**4.06**	**7.410**	**2.52**
G × N	1	228.270	0.700	0	0.002	0.000	0
Residual	16	324.530			0.550		
Filamentous algae							
Grazers	1	102.390	1.040	3.18	0.001	0.030	0
Nutrients	1	190.390	1.940	3.18	0.009	0.520	0
G × N	1	66.870	0.680	0	0.001	0.010	0
Residual	16	98.380			0.017		
Foliose algae							
Grazers	1	6.855	0.060	0	0.020	0.330	0
Nutrients	1	0.680	0.010	0	0.095	1.600	2.18
G × N	1	23.100	0.200	0	0.278	0.470	0
Residual	16	116.760			0.060		
Canopy-forming algae							
Grazers	1	131.137	1.290	0			
Nutrients	1	71.920	0.710	0			
G × N	1	103.970	1.020	1.4			
Residual	16	101.623					
Articulated coralline algae							
Grazers	1	0.053	0.000	0	0.002	0.190	0
Nutrients	1	50.650	0.790	0	0.024	2.200	0.0009
G × N	1	162.250	2.530	1.68	0.001	0.130	0
Residual	16	64.150			0.011		

Table 2. Results of 2-factor PERMANOVA of the response of assemblages observed as biomass among treatments of grazing intensity (ambient vs. reduced) and nutrient concentration (ambient vs. elevated). Data were log (x +1) transformed; **bold**: p < 0.05. Unrestricted permutation (9999 times) of raw residual data using 20 permutable units

Source	df	Morphological groups			Individual species		
		MS	*F*	p	MS	*F*	p
Grazers	1	532.040	0.229	0.94	3067.090	0.995	0.42
Nutrients	1	**6063.020**	**2.611**	**0.05**	2797.070	0.907	0.52
G × N	1	1042.250	0.449	0.78	2375.130	0.771	0.67
Residual	16	2322.110			3081.530		

Table 3. Contribution of morphological groups of algae to differences in biomass between treatments of ambient and elevated nutrients. Average dissimilarity between treatments was 61.85%

Algae	Contribution %	Cumulative %
Corticated, terete	66.66	66.66
Filamentous	15.46	82.12
Foliose	9.89	92.01

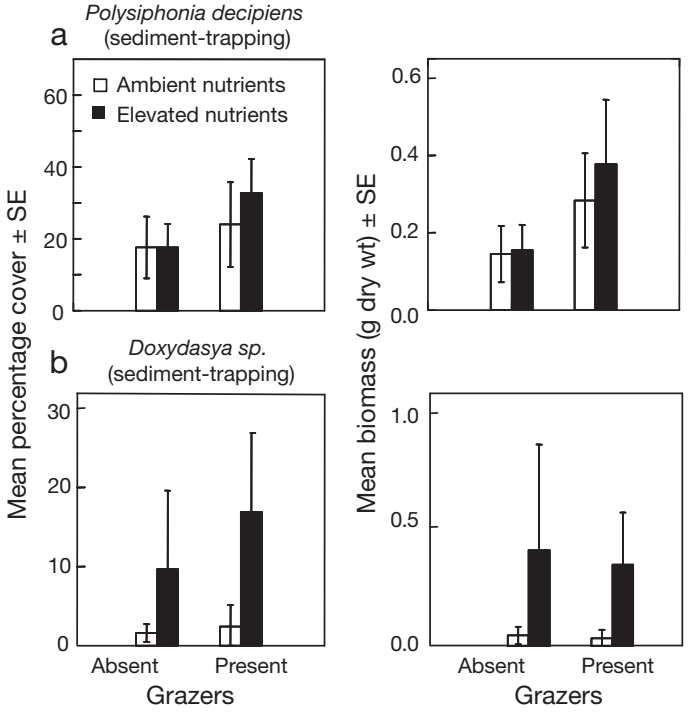

Fig. 2. Percentage cover (left) and biomass (right) (mean ± SE, n = 5) of individual algal species (a) *Polysiphonia decipiens* and (b) *Doxydasya* sp. exposed to elevated and ambient nutrient concentrations

Table 4). However, calculation of variance component for each effect suggested some trend for response to grazers (0.006–12.5), and nutrients (0.017–22.04) for *P. decipiens* and *Doxydasya* sp., respectively (Table 4).

Comparison of indices using species classification

ABC curves

The ABC curves show the impact of elevated nutrients on algal species assemblages, both with and without grazers, where nutrient enhancement causes a greater cumulative percent cover of sediment-trapping species. These algal assemblages are dominated, in abundance, by species with smaller biomass (as evidenced by the position of the biomass curve beneath the abundance curve; Fig. 3c,d). Contrastingly, in ambient conditions, algal assemblages are dominated (in abundance) by species with a greater biomass (where the biomass curve is consistently above the abundance curve; Fig. 3a,b). The latter is that expected in an assemblage that has not been subjected to water pollution, whereas the former demonstrates the dominance of smaller species (often characteristic of 'opportunistic' species, and sometimes known as 'weedy' species) in assemblages in eutrophic environments (Magurran 2004).

Shannon index

No effect of nutrient addition ($F_{1,16}$ = 0.05, p = 0.82), grazer loss ($F_{1,16}$ = 0.03, p = 0.86) or an interaction between the two ($F_{1,16}$ = 0.76, p = 0.40) was detected using the Shannon index (Fig. 4a). We detected no difference in species diversity among treatments (Fig. 4a).

Phylogenetic diversity

Greater phylogenetic diversity is indicative of a 'richer' assemblage, in terms of greater representation of higher orders of taxonomic distinction, as opposed to an assemblage of more closely related species. Under ambient nutrient conditions, phylogenetic diversity of algae decreased in the presence of grazers, indicating assemblages become less rich with the incidence of grazing. Although phylogenetic diversity was greatest (i.e. assemblages less closely related) in the absence of grazers and at ambient nutrient concentrations (Fig. 4b, Table 5: ANOVA, nutrient × grazer interaction), more importantly, where grazers were removed, diversity was significantly reduced with elevated nutrients (Table 5).

Table 4. Results of 2-factor ANOVA of abundance (% cover) and biomass (g dry wt) of species occurring in >5% of all replicates. See legend of Table 1 for details. Arcsine and ln (x + 1) transformations for *Polysiphonia decipiens* and *Doxydasya* sp., respectively, were used to reduce heterogeneity (Cochran's *C*-test not significant)

Source	df	Cover (%)			Biomass (g)		
		MS	*F*	σ^2	MS	*F*	σ^2
P. decipiens							
Grazers	1	363.070	1.980	12.5	0.090	3.220	0.006
Nutrients	1	38.520	0.210	0	0.007	0.240	0
G × N	1	68.070	0.370	0	0.004	0.130	0
Residual	16	183.470			0.028		
***Doxydasya* sp.**							
Grazers	1	116.320	0.670	0	0.001	0.010	0
Nutrients	1	648.420	3.740	22.04	0.221	0.119	0.017
G × N	1	114.960	0.840	0	0.003	0.030	0
Residual	16	173.480			0.082		

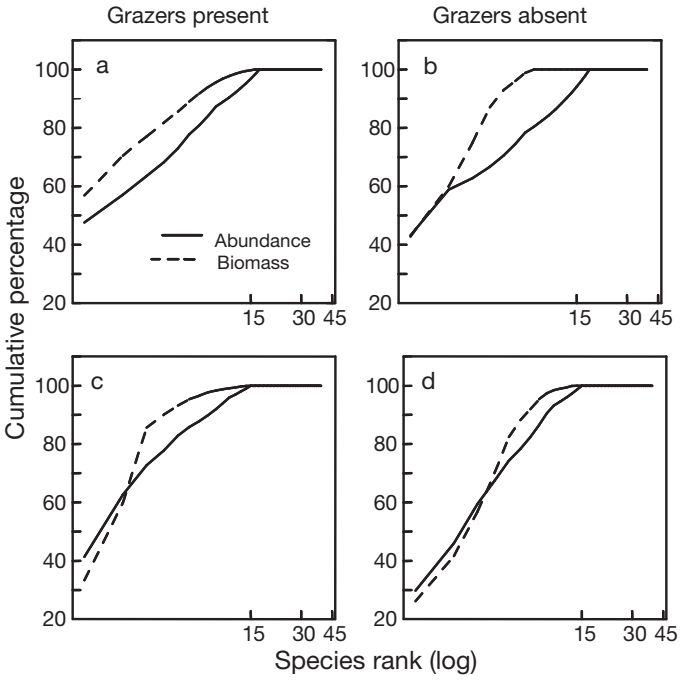

Fig. 3. Species abundance/biomass comparison curves for (a,b) ambient nutrient concentration, (c,d) elevated nutrient concentration

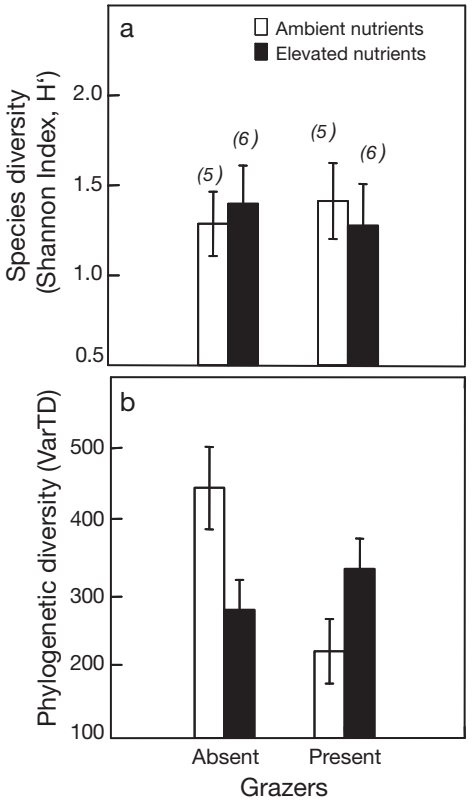

Fig. 4. Indices of species diversity (a) Shannon index and (b) phylogenetic diversity (mean ± SE, n = 5) of algal assemblages subjected to elevated and ambient nutrient concentrations, both with grazers present and absent. Values in brackets in (a) indicate the mean species richness

In terms of representative phylum, though much less abundant, phylogenetic diversity was greater for Chlorophyta and Heterokontophyta (where all species belonged to different orders) than for the dominant phylum, Rhodopyhta. Of the 22 species of red algae detected, 72% were in the order Ceramiales, 63% of which belonged to the family Rhodomelaceae. It stands to reason that assemblages with a greater representation of green and brown algal species would be richer (higher diversity) than those dominated by closely related red species. Our results show that treatments exhibiting a higher dominance of red algal species (enhanced nutrients) were correspondingly less rich. Assemblages with enhanced nutrients, both with and without grazers, had 67% and 63% occurrence of red species, respectively, compared to 52% and 56% of species in assemblages at ambient nutrient concentrations.

DISCUSSION

Our key finding was that the overall structure of algal assemblages responded primarily to nutrients, and this response interacted with grazers for some measures of habitat. Biomass responded positively to nutrients (particularly sediment-trapping algae) in the absence of grazers. Species diversity (as measured by phylogenetic diversity) was negatively impacted when grazers were absent. In this discussion, we assess the success of each measure, by classification (species versus morphology) and metric (simple versus index) against their ability to detect these changes (summarised in Table 6).

Comparison of classification (morphology versus species) with simple measures

Corticated, terete algae were the most abundant morphological group (abundance and biomass) across all experimental reefs. Although the percentage cover of these and other algae is sensitive to nutrients, and to a lesser extent grazing in this system (Russell & Connell 2005), we did not detect experimental effects when measured as percentage cover, despite the largest variance component (σ^2 = 75.46). By comparison, biomass of morphological groups, though considerably more labour intensive to analyse, was a more sensitive measure. Both univariate and multivariate analyses detected the effect of nutrient addition (i.e.

Table 5. Results of 2-factor ANOVA of phylogenetic diversity (variation in taxonomic distinctness, VarTD). SNK test is provided for the significant Grazer × Nutrient interaction. See legend of Table 1 for further details. Data conformed to the assumption of homogeneity of variance (Cochran's *C*-test) and were untransformed

Source	df	MS	*F*	p	σ^2
Grazers	1	35907.820	4.240	0.056	1372.26
Nutrients	1	3809.670	0.450	0.511	0
G × N	1	100070.260	11.820	0.003	4580.38
Residual	16	8462.650			
SNK tests on grazer × nutrient interaction					
Ambient nutrients	grazers present < grazers absent				
Elevated nutrients	grazers present = grazers absent				
Grazers present	elevated nutrients = ambient nutrients				
Grazers absent	elevated nutrients < ambient nutrients				

Table 6. The influence of method (classification and index) on the detection of treatment effects (i.e. nutrients, grazers and their interaction). The null hypothesis was rejected if $^{*}p < 0.05$ or $^{**}p < 0.005$, or ABC curves visually departed under elevated nutrient conditions

Method	Perturbation		
	Enhanced nutrients	Loss of grazers	Nutrients × grazers
Cover (%)			
Functional group	ns	ns	ns
Species	ns	ns	ns
Biomass			
Functional group	*	ns	ns
Species	ns	ns	ns
ABC curves	*	n/a	n/a
Phylogenetic diversity	ns	ns	**

increases in dry weight of corticated, terete algae) on dry weight. This result suggests that using the single measure of percentage cover as a basis for detecting the impact of altered environmental conditions may not always reliably detect the effects of treatments.

While the capacity to detect and predict community response is hoped to improve with the use of morphological groups (Hay 1994, Steneck & Dethier 1994), we were unable to detect the effect of treatments on such groups, except as biomass. Nevertheless, such groupings may usefully describe assemblages that can vary in proportion, according to water quality (Benedetti-Cecchi et al. 2001, Gorgula & Connell 2004, Petchey & Gaston 2006). While the morphological group approach can result in considerable loss of information, understanding responses at broader levels of biological organisation may provide lessons than transcend alternate systems.

Estimates of species abundance (percent cover and biomass) did not differ among treatments. It is possible that large variation in abundance reduced the capacity to detect a response, as almost 50% of species were sampled only once across all treatments. Experiments are invariably constrained by logistics, and our results, using replication typical for ecological experiments (i.e. 2 crossed factors, each with 2 levels, and n = 5), indicate the difficulty in detecting the effect of experiments on the percentage cover or biomass of individual species relative to broader levels of biological organisation (i.e. morphological groups). It is notable, therefore, that the use of broader morphological groupings may reduce variation, and may therefore be more sensitive to treatments where experimental replication is constrained. If almost half the species only occurred in 1 replicate, but their constituent group occurred predominantly in 1 treatment, effects may be more readily detected. These effects would be meaningful where the effects can transcend the idiosyncratic responses of individual species (Hay 1994) and thereby have implications for community composition rather than minute differences between species-specific responses.

In this study, the 2 most frequently occurring species (with >5% occurrence) among all replicates were *Polysiphonia decipiens* and *Doxydasya* sp. Although both species share the same morphological group (corticated, terete algae) they had opposing responses to grazing and nutrients. Grazing had the greater influence on *P. decipiens* (percentage cover: $\sigma^2 = 12.5$ and biomass: $\sigma^2 = 0.006$, Table 4), whereas nutrients had the greater influence on *Doxydasya* sp. (percentage cover: $\sigma^2 = 22.04$ and biomass: $\sigma^2 = 0.017$). Variation within morphological groups is one of the problems associated with their use because classifications based on morphology do not necessarily reflect similar ecological responses (Padilla & Allen 2000). Grouping by morphology or function ultimately represents the sum of species responses within the group, both positive and negative. The inability to detect an effect with morphological groupings, therefore, may not necessarily be due to the disturbance having no effect, but rather the potentially high variation in species-specific responses within a morphological group.

Comparison of indices using species classification

ABC curves as an index

Until now, ABC curves have been applied to infaunal polychaetes. Our study demonstrated that the relationship and position of the ABC curves can imply a pollution response within benthic algal assemblages. Inde-

pendent of grazer density, the abundance of large- and small-bodied species differed under enhanced nutrients. Under ambient nutrient concentrations, species of greater biomass were most abundant (e.g. *Doxydasya* sp., *Liagora* sp.), whereas under enhanced nutrient concentrations, species of smaller biomass were more abundant (e.g. *Cladophora* sp., *Herposiphonia* sp.). This change is characteristic of polluted environments (Magurran 2004).

Anthropogenic increases in nutrient loading promotes rapid growth of opportunistic algae and a decline of more complex canopy-forming algae (Worm & Sommer 2000, Nielsen 2003, Gorgula & Connell 2004). As such, smaller fast-growing species typically dominate polluted environments (McClanahan 1997) and are considered 'weedy', proliferating in conditions unfavourable to more complex species (Tilman & Lehman 2001). While ABC curves traditionally incorporate counts of individual invertebrates within benthic cores in order to detect a response to pollution, the deviation of our ABC curves, and subsequent reversal of communities to dominance by smaller species, indicates the potential use of ABC curves for detecting responses in algal assemblages.

Shannon index of diversity

A well understood disadvantage of the Shannon index is the bias created by its reliance on sampling effort, where error arises by insufficiently sampling all species in a community (Lande 1996). The Shannon index was not sensitive enough to detect treatment effects that were evident with ABC curves (i.e. greater abundance of weedy species under enhanced nutrient conditions). However, as this index is based on the abundance of particular species, analysis was limited to taxa that were directly sampled using the point-intercept method. Of the 39 species sampled across all treatments, 10 were identified during secondary sampling (taxa that did not fall under the original point-intercept sampling), and therefore abundance sampling did not include all species in the community.

Phylogenetic diversity as an index

Theory suggests that assemblages with fewer species are indicative of disturbed systems; e.g. elevated nutrients often result in a considerable loss of plant species (Tilman & Lehman 2001, Steneck et al. 2002). Although our results show no sensitivity of species diversity to perturbations (Shannon index), the measure of phylogenetic diversity of assemblages (taxonomic distinctness) detected an interaction between the loss of grazers and the decline in water quality (i.e. enhanced nutrients). Where grazers were removed, assemblages exposed to elevated nutrients were 'less rich' (in terms of the constituent species being more closely related). This interaction between grazers and nutrients explains a substantial proportion of variation among treatments ($\sigma^2 = 4580.38$), equating to 31.7 % of the magnitude of effect. Where herbivore densities are reduced and nutrients are enhanced, these stressors may accelerate assemblages toward monopolies of more closely related species.

In conclusion, our ability to detect the experimental effects of treatments was mediated by the response variables used to observe benthic habitat. Relative to observations of species as traditional units (i.e. percentage cover and biomass), observations of morphological groups (i.e. biomass) provided greater capacity to detect the effects of nutrient enhancement. Indices of species level observations (i.e. phylogenetic diversity) were sensitive to the combined effects of nutrients and grazers. This uneven ability to detect change demonstrates the extent to which the choice of response variables can predetermine our perception of human-driven change. By understanding which combination of classifications and indices are most sensitive to particular environmental influences, we may improve our ability to identify and anticipate the ecological consequences of human activities.

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Appendix 1.

Papers reviewed were sourced from 14 journals between 1993 and 2006 inclusive. They included Marine Biology, Journal of Experimental Marine Biology and Ecology, Biological Bulletin, Aquatic Botany, Marine Ecology Progress Series, Journal of the Marine Biological Association of the United Kingdom, Journal of Phycology, Australian Journal of Marine and Freshwater Research, Estuarine Coast and Shelf Science, Aquaculture, Phycologia, Marine Pollution Bulletin, Journal of Planktonic Research and Journal of Sea Research. The search was limited to marine and freshwater research journals, using the keywords 'field' and 'experiment', and studies were selected if they used manipulative experiments to test assemblage responses.

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