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Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management

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Abstract

Habitat mapping at the scale at which marine protected areas are designed and managed is essential for assessment of, and design for, representation. Most habitat mapping studies rely solely or in part on abiotic surrogates for patterns of biodiversity. The utility of abiotic variables in predicting biological distributions at the local scale (10s of km) was tested in a remote video survey of macrobenthos in Moreton Bay, Australia. Habitat classifications of the same set of 41 sites based on 6 abiotic variables and abundances of 89 taxa and bioturbation indicators were compared using correlation, regression and ordination analyses. The concepts of false homogeneity (abiotically similar but biologically distinct) and false heterogeneity (abiotically distinct but biologically similar) were defined to describe types of errors associated with using abiotic surrogates to construct habitat maps, and quantified using two separate methods. Overall, the best prediction by abiotic surrogates explained less than 30% of the pattern of biological similarity. Errors of false homogeneity were between 20% and 62%, depending on the methods of estimation. Predictive capability of abiotic surrogates at the taxon level was poor, with only 6% of taxon/surrogate correlations significant. Abiotic variables did not discriminate sufficiently between different soft bottom communities to be a reliable basis for mapping. These results have implications for the widespread use of abiotic surrogates in marine habitat mapping to plan for, or assess, representation in marine protected areas. Little confidence can be placed in marine habitat classifications based solely or largely on abiotic surrogates without calibration by rigorous biological surveys at the appropriate scale. Therefore, it is questionable whether marine protected areas designed on this basis can have measurable benefits for conservation.

Keywords: Marine protected areas; Video survey; Abiotic surrogates; Representation; Moreton Bay; Australia

1. Introduction

Planning and design of marine protected areas over the last decade has increasingly adopted the concept of representativeness as a major criterion, including its use in IUCN guidelines for highly protected areas (IUCN, 1994). Representativeness in this case means the desire of planners to incorporate samples of each habitat, landscape or community type, depending on the scale of the marine protected area and the issues being addressed.

Representation can be assessed within a nested series of scales from continental (1000 km) to site (1 km). Kelleher et al. (1995) produced a continental scale classification of marine environments. In some parts of the world, including Canada, Australia and South Africa, regional scale (100 km) classifications have been produced as a basis for establishment of marine protected area systems (e.g. Hockey and Branch, 1997; Interim Marine and Coastal Regionalisation of Australia Technical Group, 1998; Zacharias and Howes, 1998).

For highly protected areas (Category II or above, IUCN, 1994), which contain the core values of most marine protected areas including multiple-use examples, polygons are generally drawn at the local scale (10 km) or smaller (Stevens, 2002). Planning for, or assessment

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of, representation cannot logically be carried out without the crucial step of habitat mapping at the requisite planning scale. Classification and mapping of marine habitats at the local scale has not been widely done, generally due to the (actual or perceived) lack of available information, and the expense associated with subtidal surveys. Therefore, current classifications done at this scale (e.g. Zacharias et al., 1999) rely heavily on abiotic surrogates, rather than directly reflecting biological distributions.

Abiotic data lend themselves well to habitat classification exercises because they often come in mapped form (e.g. from remote sensed imagery), or are already georeferenced (e.g. sediment samples with co-ordinates attached). A recent trend is the use of sophisticated sonar systems to classify the seabed on the basis of physical properties deduced from analysis of the returning acoustic signal (e.g. Davies et al., 1997). In basing habitat mapping for the purpose of representation on abiotic surrogates, it is implicitly assumed that the surrogates predict, or at least correlate with, patterns of biological distributions reasonably well. This assumption is not often tested.

In some cases, abiotic variables have proved to be good predictors. Long et al. (1997) found that current stress predicted the distribution of epibenthos in Torres Strait (between Australia and New Guinea). Zacharias and Roff (2001) reported that a combination of salinity, temperature and fetch predicted intertidal species richness in British Columbia. Both of these studies were at the regional scale, and are not directly applicable to representation of habitats within marine protected areas at the local scale.

Recent calls in the literature for improved rigour in marine protected area design (Agardy, 1995; Stevens, 2002) demand reasonable confidence in the accuracy of habitat mapping for representation. If abiotic surrogates for patterns in biological distributions are used, two types of errors are possible: *false homogeneity*, where sites with similar or identical abiotic (geophysicochemical) conditions support different biological distributions, or *false heterogeneity*, where sites with different abiotic conditions support very similar biological distributions. Both types represent an inability of analyses that are based on abiotic conditions to model biological distributions accurately. Habitat mapping (and subsequent management decisions) based on abiotic variables subject to these errors will necessarily be inaccurate and misleading. This may be ameliorated by extensive ground truthing, however in subtidal areas this is expensive and logistically difficult. It could be argued that the additional survey effort required to ground truth accurately the predictive power of abiotic surrogates would be better spent directly surveying the biota, since they are of primary interest in planning for representation in marine protected area design.

A recently completed remote underwater video survey in Moreton Bay, Australia, provided an opportunity to compare biological and abiotic data at the scale used by marine protected area designers and managers. The aims of this study were to:

- determine the predictive ability of abiotic variables for observed patterns in biological distributions;
- quantify the frequency of errors of false homogeneity and false heterogeneity and thereby;
- assess the utility of abiotic information in habitat mapping for representation in marine protected area design at this scale.

2. Methods

2.1. Study site

Moreton Bay (27°15′S, 153°15′E) on the east coast of Australia, is a shallow coastal embayment, covering approximately 1,500 km^2 (Fig. 1). The bay is protected on the eastern side by Moreton and North Stradbroke Islands, with its main ocean entrance in the northeast. It is approximately 35 km wide at the widest point, and narrows in the south into a maze of mangrove-fringed waterways. Most of the bay is less than 15 m deep, but reaches depths greater than 25 m in the north eastern

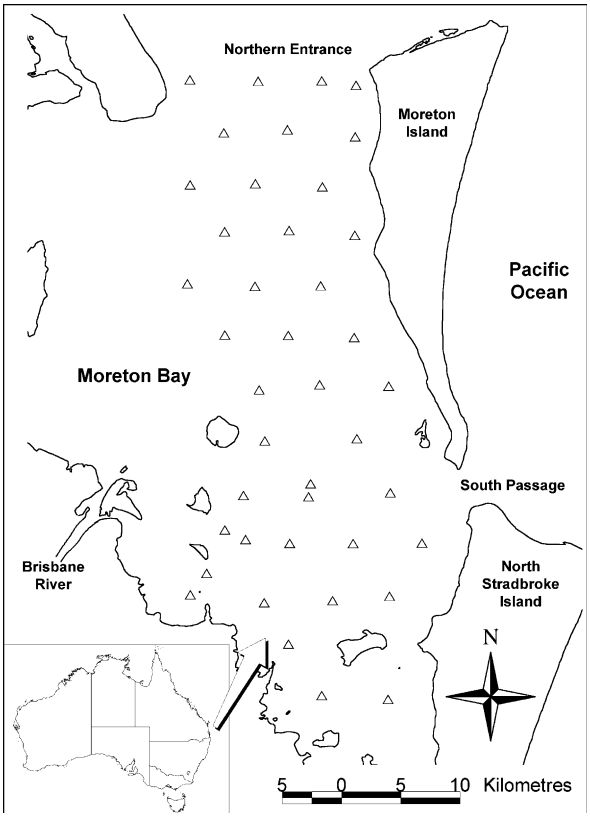

Fig. 1. Location of study area with sample sites (△).

part, adjacent to the main ocean entrance. The drainage catchment is substantial (21,000 km^2) and contains urban centres with populations of about 1.5 million people (Dennison and Abal, 1999). The western parts of the bay are heavily influenced by terrestrial inputs of sediment and nutrients (Costanzo et al., 2001) dominated by inputs from the Brisbane River (Eyre et al., 1998) plus 3 smaller river systems. The eastern side is essentially under oceanic influence (Udy and Dennison, 1997), with ocean entrances in the north and east.

The bay and adjacent offshore waters are included within Moreton Bay Marine Park, a zoned multiple-use marine protected area declared in 1993 and managed to "provide for the ecologically sustainable use of Moreton Bay Marine Park and to protect its natural, recreational, cultural heritage and amenity values" (Anon, 1997, p. 9).

Sample sites for both abiotic and biological data were set out in a staggered 5 km spaced array covering the central, eastern, and southern parts of the bay (Fig. 1). The 5 km spacing was chosen to facilitate construction of polygons of relative similarity at the local (10 km) scale. The western portions of the bay were not included because they are generally too turbid for video-based survey.

2.2. Abiotic datasets

Contemporary studies were examined to determine a typical suite of abiotic variables used to construct habitat classifications (e.g. Bax and Williams, 2001; O'Hara, 2001; Zacharias and Roff, 2001). It should be noted that such studies may be carried out by government agencies or non-government organisations, and are often only reported in internal documents or limited circulation reports (e.g. Partnership for Interdisciplinary Studies of Coastal Oceans, 2002 in Litt.; Marine Reserves Working Group, 2000 in Litt.).

Variables could be grouped into three themes; those concerned with the nature of the substrate (depth, sediment type [mud, sand, gravel, rock], sediment constituents [e.g. carbonate fraction]); the nature of the water body overlying the substrate (temperature, pH, salinity, turbidity), and influences on the local environment (exposure, current velocities, proximity to major river entrances, nutrient inputs). These operate at a range of scales and not all were relevant to this study. From examining the suitable information available for Moreton Bay, a suite of variables was selected as the basis for an abiotic classification of the bay.

The variables selected were: depth, mud content of sediment, sand content of sediment, reversing tidal current velocity, residual current velocity, distance from Brisbane River mouth, distance from northern oceanic entrance, distance from eastern oceanic entrance (South Passage), fetch from southeast direction, and fetch from northeast direction (major prevailing winds).

The 41 sites used for the biological surveys (locations determined as the mid-point of each transect – see field methods below) were scored for each of the variables. From this initial matrix, variables were combined or eliminated to give equal weight to variable types, and avoid redundancy. Correlation analyses were used to highlight areas of potential overlap. Mud and sand content were reduced to a single variable since they are almost exactly the reciprocal of each other, and the second therefore adds no additional information to the analysis. The two current variables were highly correlated and subsequently reduced to a single variable. The distances to the two ocean entrances were reduced to a single variable, weighted by the ratio in cross-sectional area between the northern and eastern entrances, to allow for the much greater flow volume through the northern entrance (Dennison and Abal, 1999). Fetch variables were combined (root sum of squares) to give an index of exposure. The final abiotic matrix was therefore 41 sites by 6 variables (Table 1) all standardised to the range 0–1 to give equal weight.

Some variables that have been used in other studies (e.g. Zacharias and Roff, 2001), such as tidal range,

Table 1
Variables for abiotic classification

Variable	Units	Definition	Source
Depth	m	Corrected to low water datum	As measured
Mud fraction	%	Fraction of total sediment, 10 classes, spatial extrapolation (contour plot) from point data.	Dennison and Abal (1999)
Current velocity	$m\,s^{-1}$	Five classes	Dennison and Abal (1999)
Distance to River	km	Direct measurement from site to midchannel point at Brisbane River mouth	AUSLIG 1:250,000 digital mapping
Distance to Ocean	km	$Dn + (Dsp * R)$	AUSLIG 1:250,000 digital mapping
Fetch	km	$\sqrt{(Fne^2 + Fse^2)}$	Queensland Department of Transport charts

Dn, direct measurement from site to closest point on closing line across northern entrance.
Dsp, direct measurement from site to closest point on closing line across south passage
R, ratio of approximate cross-sectional areas (south passage/northern entrance).
Fne, distance to nearest land or drying bank in NE direction.
Fse, distance to nearest land or drying bank in SE direction.

salinity and temperature, were not used because they were considered to be either almost uniform over the whole of the study area, or functions of other variables already included (e.g. Distance to Ocean). Other common variables (slope and form of rocky shores) are applicable to intertidal studies but not to the present, wholly subtidal, and wholly soft-bottom, investigation. Terrestrial influences such as nutrient loads and pollutant volumes were not included because several studies (Gabric et al., 1998; Dennison and Abal, 1999; Costanzo et al., 2001) show that these factors rarely penetrate into the eastern side of the bay, the effects remaining concentrated on the western bay.

2.3. Biological datasets

2.3.1. Field methods

Surveys were carried out using a towed self-adjusting array developed especially for the study following the design principles of Barker et al. (1999) but much reduced in size and complexity. It had the advantage of being small and lightweight, and therefore easily deployed from a small vessel, in this case a 5.75 m open boat. It was relatively low-cost, using off-the-shelf consumer-level technology, and had virtually no impact on the area surveyed. Cost of the in-water component was less than 1000 Australian dollars.

The array was towed on a 10 m tether behind a dropweight suspended beneath the survey vessel. It was slightly positively buoyant but maintained a constant distance of 1 m above the bottom by trailing a 2 m length of light chain. This system allowed the array to self adjust to irregularities on the bottom, and coped better with rough terrain than sled-mounted arrays, which are at risk of entanglement and damage. The array was also smaller and lighter than a sled of similar elevation, and more flexible, in that it could be configured to fly at different elevations by changing the weight of the drag chain.

The video sensor was a compact, high resolution (480 lines) colour analogue camera in PAL format, measuring only 7 cm long and 2 cm in diameter. The unit was powered and the video signal returned to the surface via 3-core cable. Video was recorded at the surface on a Sony Digital-8 handycam that doubled as video monitor with its 6.5 cm colour LCD screen. Two laser diodes projected dots onto the bottom a known and constant distance apart to allow calibration of the video images, and check for correct orientation and elevation of the array.

Preliminary studies with this video sampling method showed that a single long transect gave equivalent results in species richness, assemblages and abundance to the more conventional technique of using multiple replicate transects. This ''replication through length'' approach had substantial practical advantages for boat-based surveys, and allowed a single 500 m transect to be run at each site. Transects were located using GPS, which gave sufficient positional accuracy (about 15 m) compared to the spacing of the sample points. Surveys were carried out between September and November 2002.

2.3.2. Data extraction

Digital video was captured at 1 frame every 2–5 s, the frame rate giving maximum coverage without frame overlap. The resultant frame series was stored as a Quicktime movie file, and digital image enhancement carried out where necessary to enhance clarity and contrast.

Overlay layers were added to the Quicktime movies to facilitate data extraction. A calibrated 1 m^2 frame was overlaid, within which all solitary or discrete colonial organisms were counted, as well as a 9-point array for calculating % cover. For each frame, the taxa present at each of the nine points was recorded, as was the number of individuals of each taxon in the whole frame. Taxa were visually identified to morphospecies. Presence and abundance of bioturbating organisms was quantified by scoring variables for occurrence of biogenically worked sediment surfaces, and counts of burrows or holes in three size classes.

Data were pooled for all frames in a transect. Percent cover was calculated from point data, and density calculated from count data and bioturbation indicators. A uniform standardisation technique was used to allow cover, count and bioturbation indicator data to be analysed as a single dataset. Each of these data types was separately scaled into the range 0–1 and then combined. Preliminary analyses (Stevens unpubl.) showed than patterns of between-site similarity were insensitive to differences in scale between the data types of up to two orders of magnitude. The resulting data matrix (morphospecies and bioturbation indicators by sites) was then analysed using multivariate techniques.

2.4. Analysis

2.4.1. Multivariate classification

Abiotic similarity matrices were derived using the widely used Normalised Euclidean Distance. Biological similarity matrices were produced for both untransformed and fourth-root ($\sqrt{\sqrt{}}$) transformed data (to allow for the influences of both abundant and rarer taxa in the dataset) using Bray-Curtis similarity, widely considered the most appropriate measure for biological information because it ignores conjoint absences (Clarke, 1993).

2.4.2. Whole dataset comparisons

The correlation between abiotic and biological similarity matrices was tested using Spearman's correlation

coefficient and Mantel's test. The correlation coefficient values indicate how well abiotic similarity matches observed biological similarity. Mantel's test (Manly, 1997) is a similar procedure but uses a more stringent test statistic. Predictive ability of the abiotic similarity matrices was further tested by regression analysis to give a measure of the amount of the variance explained by the relationship. For each of these measures (Spearman's correlation, Mantel's test and regression) the use of standard statistical tables to determine significance is considered invalid because the elements of the similarity matrices cannot be considered independent. Significance was therefore estimated using Monte Carlo randomisation (Manly, 1997).

An iterative approach was used whereby similarity matrices from different combinations of the six variables were compared to those from the biological data to find the set of abiotic variables with the best predictive power.

2.4.3. Extremes of abiotic similarity

Whilst it might be expected that there is some error in matching abiotic and biological similarity for site-pairs with intermediate similarity values, at the extremes of the abiotic similarity distribution there should still be reasonable predictive capacity. The first method of quantifying errors of false homogeneity and heterogeneity was therefore by examining the 10% most similar and 10% most dissimilar site pairs from abiotic data to see if these were also biologically very similar (or dissimilar). The 820 site-pairs in the similarity matrices were ranked on the basis of abiotic similarity and the most abiotically similar 10% selected for further analysis. The biological similarity values for each of these site-pairs were examined to determine the proportion that were biologically similar (see Fig. 2 for a diagrammatic explanation of this analysis). Several levels of similarity were used to give a range of measures of error. Within the most abiotically similar 10%, the frequency of occurrence of site-pairs with Bray-Curtis similarity scores above each of the 90th, 75th, 50th, 25th and 10th percentiles was determined. Similarly, pairs of sites that were the 10% most different in abiotic terms were examined to determine the proportion of these that were clearly biologically distinct.

2.4.4. Derived group comparisons

The 41 sites were classified into groups for both abiotic and biological similarity measures on the basis of cluster analysis and MDS ordinations. Several solutions were examined for each measure, from two to six groups. The makeup of the groups at each solution was compared and each site scored as to whether it was grouped consistently using abiotic and biological similarity measures. Sites not grouped consistently were considered errors of prediction and assigned to either

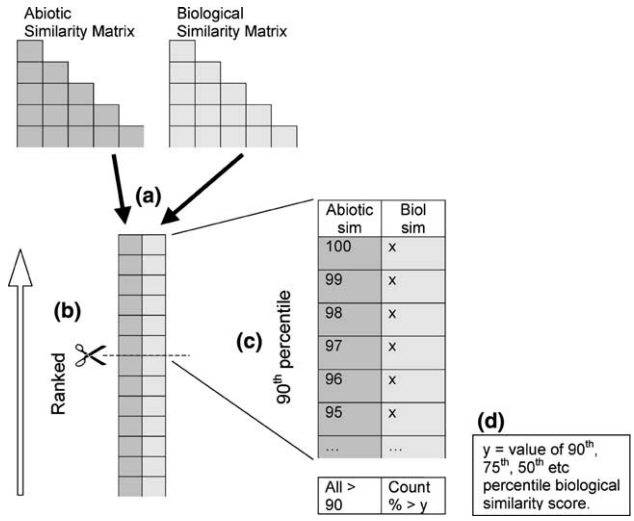

Fig. 2. Method for extremes of abiotic similarity (Top 10%) analysis. Steps: (a) Construct similarity measures by site-pairs matrix; (b) rank matrix by abiotic scores; (c) select site pairs with abiotic similarity scores above 90th percentile; (d) count number of site pairs within the selected set that have biological similarity scores above selected interpretation level (90th, 75th, 50th, 25th, 10th percentiles). Repeat (c) and (d) with abiotic similarity scores below 10th percentile for bottom 10% analysis.

false homogeneity or false heterogeneity, depending on the nature of the error. The proportion of the 41 sites that constituted each type of error was determined for each solution between two and six groups.

2.4.5. Influence of individual abiotic variables

Correlation and forward stepwise multiple regression analyses were used to determine which, if any, of the abiotic variables could predict the following variables: (1) number of species, (2) the abundance of individual taxa or bioturbation indicators, and (3) abundance of organisms within pooled groups, % cover (estimated from point array), solitary or discrete organisms (density from count per unit area), or bioturbation indicators data (burrow counts in three size classes plus occurrence of biogenic working).

3. Results

3.1. Description of biological distribution dataset

Over 20 km of video transects were recorded, and 7745 individual frames analysed. Mean number of frames per transect was 189 (range 65–323). Relative abundances (as percent cover or density) of 85 morphospecies in 10 phyla, plus four indicators of bioturbation, were recorded. Phyla represented were chlorophyta, phaeophyta, rhodophyta, trachaeophyta (seagrasses), porifera, cnidaria (anthozoans, corals),

annelida, mollusca, echinodermata and chordata (ascidians). Of the 85 morphospecies, 18 occurred in only one site, and 34 occurred in more than 10% of sites. Three morphospecies were very common (Seagrasses *Halophila spinulosa* and *Zostera capricorni*, Anemone *Cerianthus* sp. 2), each contributing more than 10% to total standardised abundance. However, these common morphospecies were not widespread over the study area, and none occurred in more than 20% of sites. No morphospecies or bioturbation indicator was ubiquitous. The most frequently occurring morphospecies (the short quill seapen *Virgularia gustaviana*) occurred in 42% of sites but contributed less than 0.2% to total standardised abundance. Bioturbation was frequent, with small burrows (<3 cm in diameter) and medium burrows (3–10 cm) both occurring in 68% of sites.

3.2. Whole dataset comparisons

Iterative classifications using different combinations of the six abiotic variables showed that the best correlation with the biological datasets used all six variables. Spearman's correlation between abiotic and biological similarity from $\sqrt{}\sqrt{}$transformed data gave $\rho = 0.56$ ($p < 0.001$), slightly better than the correlation with biological similarity from untransformed data ($\rho = 0.51$, $p < 0.001$). Correlation values >0.5 with high significance suggested that the classification using all six abiotic variables would be a moderately good predictor for biological similarity.

Mantel's test also showed that there was a statistically significant relationship between abiotic and biological similarity from $\sqrt{}\sqrt{}$transformed data ($r = 0.26$, $p < 0.001$) and between abiotic and biological similarity from untransformed data ($r = 0.18$, $p = 0.030$). The standardised Mantel statistic, r, has a range from 0 (no relationship) to 1 (perfect match), so the values found suggested only a weak relationship.

Although regression analyses showed that there was a positive relationship between abiotic and biotic similarities (in every case $p < 0.01$), R^2 values were low. Abiotic similarity predicted biological similarity from $\sqrt{}\sqrt{}$transformed data with $R^2 = 0.28$, and the R^2 value was only slightly improved by applying transformations to the y-axis ($R^2 = 0.29$). Predictive ability of abiotic similarity for biological similarity from untransformed data was lower still ($R^2 = 0.13$). At best, therefore, the abiotic variables explain <30% of the corresponding biological similarity.

3.3. Extremes of abiotic similarity

Only biological similarity from $\sqrt{}\sqrt{}$transformed data was used in this and subsequent analyses, since it was better predicted by the abiotic variables than that from untransformed data. Of the 82 most similar site pairs, less than 40% had biological similarity scores above the 90th percentile (Table 2). Less than 70% had biological similarity scores above the 75th percentile, and about 90% of these very similar sites had Bray-Curtis scores above the median.

Of the 82 most abiotically dissimilar site pairs, 10% were actually somewhat biologically similar (Bray-Curtis scores above the median). Only 45% of these very abiotically dissimilar sites had Bray-Curtis scores in the bottom 10%, and less than 70% had Bray-Curtis scores below the 25th percentile (Table 2).

Estimates of the risks of false homogeneity and false heterogeneity can be derived from these results, depending on how stringent a test is required (Table 3 and Fig. 3). If a close match is required (10% rule), false homogeneity was predicted by abiotic data in 62% of abiotically very similar site pairs examined. Even at a less stringent interpretation (25% rule), false homogeneity was predicted in 32% of abiotically very similar site pairs. At the broadest interpretation, false homogeneity is predicted in about 10% of abiotically very similar site pairs. The risk of false heterogeneity was a little lower than that of false homogeneity at the most stringent interpretation (Table 3) but was similar at less stringent interpretations.

Table 2
Proportion of biological similarity at extremes of abiotic similarity

Abiotic	Biological	Proportion included (%)
Very similar site pairs (top 10%)	Top 10%	38
	25%	68
	50%	92
	75%	99
	90%	100
Very dissimilar site pairs (bottom 10%)	Bottom 10%	45
	25%	67
	50%	90
	75%	100
	90%	100

Total number of site-pairs was 820, and n for each 10% was therefore 82.

Table 3
Estimates of error (derived from Table 2)

Factor	Error of false homogeneity (%)	Error of false heterogeneity (%)
10% rule	62	55
25% rule	32	33
50% rule	8	10

Errors represent the proportion of biological similarity not included at extremes of abiotic similarity, and are therefore the inverse of values in Table 2. Errors of false homogeneity are derived from the top 10% abiotic similarity analysis and errors of false heterogeneity are derived from the bottom 10% abiotic similarity analysis.

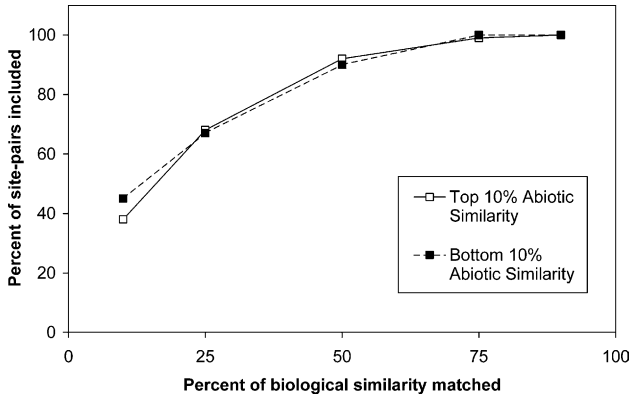

Fig. 3. Matching abiotic and biological similarity at extremes of abiotic similarity. Percentage of site pairs within the highest and lowest 10% of abiotic similarity values which have biological similarity values above the ranges shown on the *x*-axis.

3.4. Derived group comparisons

An MDS ordination plot coded for both abiotic and biological datasets (Fig. 4) at a four group solution shows the relatively poor match between the composition of derived groups. ANOSIM analysis verified that derived groups were significantly different from each other for both abiotic (global $R = 0.74$, $p = 0.001$) and biological datasets (global $R = 0.87$, $p = 0.001$. When plotted on the site co-ordinates (Fig. 5) the differences in spatial relationships between abiotic and biological datasets are clear.

At the extremes of the available set of group number solutions, 1 and 41 groups, the abiotic and biological group plots will match exactly. At intermediate values the error will vary. At solutions with more than six groups, the cluster and ordination plots began to drop off single sites, rather than discrete sub-groups, and group comparisons therefore became increasingly difficult to interpret. The error in abiotic prediction was at its greatest (50–60%) for four and five group solutions (Table 4). The majority of the error was false homogeneity, with false heterogeneity remaining relatively low and quite constant (Table 4).

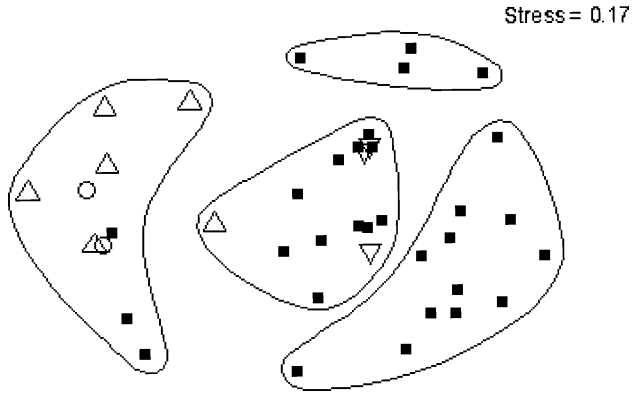

Fig. 4. Comparison of groups from abiotic and biological classifications at 4 group solution. MDS ordination plot of biological classification (Bray-Curtis similarity from $\sqrt{}\sqrt{}$transformed biological data). Biological group membership at 4 group level indicated by polygon boundaries. Abiotic group membership at 4 group level indicated by symbols.

3.5. Influence of individual abiotic variables

In this section multiple variables are always listed in descending order of partial correlation coefficients. Species richness of sites was found to be predicted, but not well, by a combination of depth, Distance to Ocean and Mud fraction (log-transformed *y*-axis, $R^2 = 0.34$, $p < 0.001$). Only about 6% of individual taxa or indicators correlated with abiotic variables (Table 5). The strongest relationship (highest R^2) was the prediction of frequency of biogenic working of the sediment by a combination of Mud fraction and Distance to Ocean ($R^2 = 0.30$, $p < 0.001$). The highest R^2 for a taxon predicted by abiotic variables was density of the heart urchin *Lovenia* sp. by Distance to Ocean ($R^2 = 0.28$, $p < 0.001$). Other results of note were density of bivalve sp. 2 by depth and Distance to River ($R^2 = 0.21$, $p = 0.002$) and density of the spoilt seastar *Astropecten veppa* by Fetch ($R^2 = 0.198$, $p = 0.004$). However, for the overwhelming majority of the 89 taxa observed in the biological data set there was no detectable relationship with any of the abiotic variables (Table 5). Even where significant relationships were detected, most of these had little predictive power ($R^2 < 0.2$). Distance to ocean was the variable having most relationships with individual taxa (Table 6), with more than twice the number of correlations of any other variable, yet even for this variable relationships existed with only 18% of the 89 taxa or indicators.

Of the three sets of data types, cover organisms, solitary or discrete organisms and bioturbation indicators, only cover organisms were predicted by any abiotic variables. Total cover was best (but not well) predicted by a combination of depth and Distance to Ocean (log-transformed *y*-axis, $R^2 = 0.418$, $p < 0.001$).

4. Discussion

While there is clearly a relationship between abiotic variables and biological distributions, the abiotic variables explain a relatively small proportion of the overall pattern. The whole matrix analysis showed that, at best, abiotic similarity explained <30% of the pattern of observed biological distributions. It might be expected that at the extremes of the abiotic similarity values there may be reasonable predictive capacity. Yet at the tails of the abiotic similarity distribution (top and bottom 10%), errors of false homogeneity and false heterogeneity were

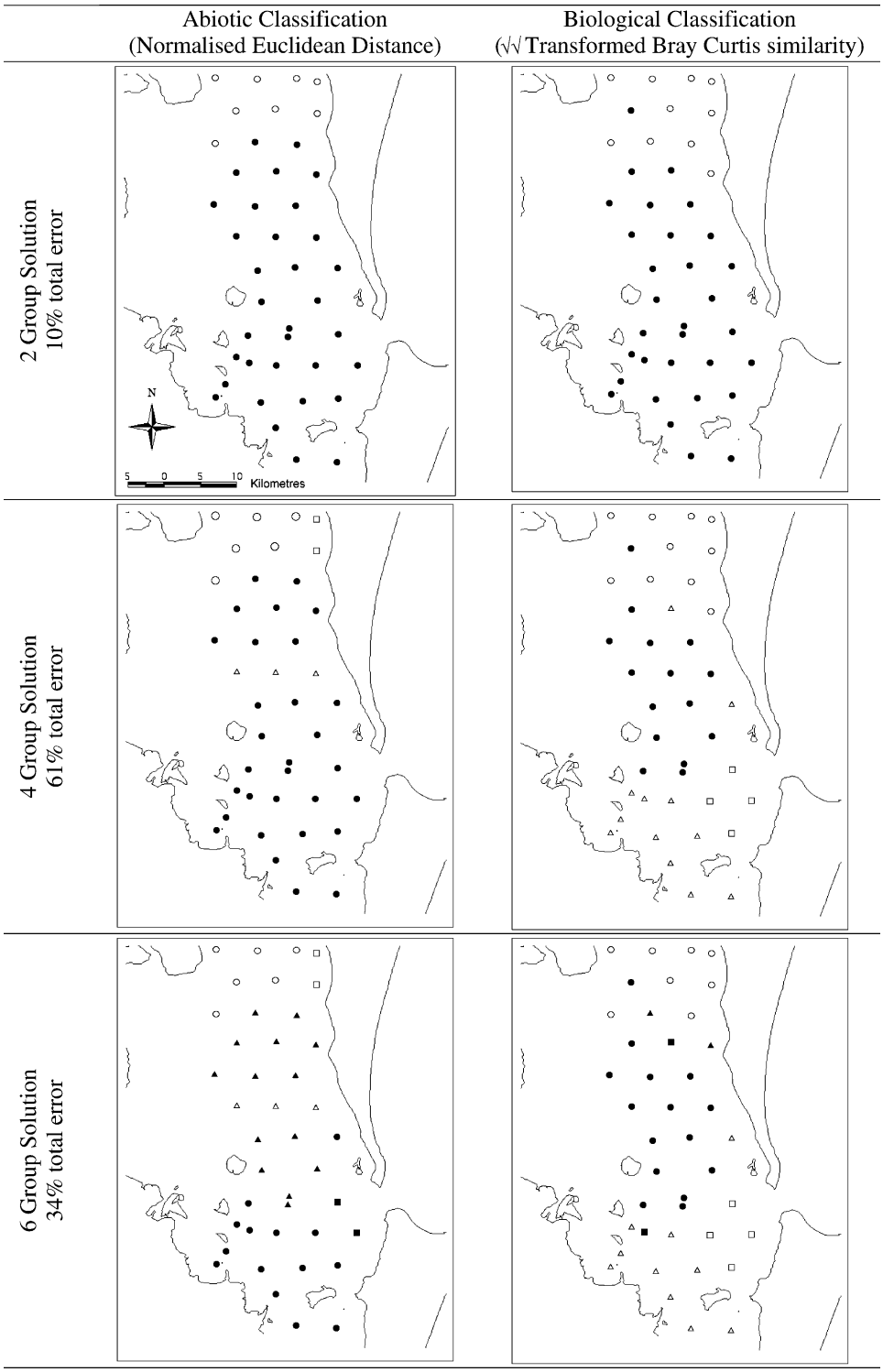

Fig. 5. Comparative maps of abiotic and biological classifications at 2, 4 and 6 group solutions. Symbols denote group membership.

large. A similarly poor match was found in comparing group membership derived independently from abiotic and biological data. At solutions with intermediate numbers of groups (4–6), errors of false homogeneity were large although errors of false heterogeneity were lower and more consistent than in the previous analysis.

Abiotic variables were also shown to have poor predictive capacity for individual taxa or indicators. The abiotic variable Distance to Ocean had the most value as a predictor, but still showed significant correlations with less than a fifth of taxa or indicators. While this supports the finding of Udy and Dennison (1997) that the eastern

Table 4
Comparison of group composition from abiotic and biological classifications

Solution no. of Grps	No. of sites consistent	Errors		
		False homogeneity %	False heterogeneity %	Total %
2	37	10	0	10
3	31	20	5	25
4	16	49	12	61
5	18	44	12	56
6	27	22	12	34

Errors are expressed as % of total number of sites (41).

False homogeneity = sites predicted by the abiotic classification to be in the same group, but the biological classification placed them in different ones.

False heterogeneity = sites predicted by the abiotic classification to be in different groups but the biological classification placed them in the same one.

Table 5
Number of individual taxa or indicators predicted by abiotic variables

	Relationship	No. of correlations	%
Significant correlations	($p < 0.05$)	33	6.2
	$R^2 > 0.1$	28	5.2
	$R^2 > 0.2$	2	0.4
	$R^2 > 0.3$	1	0.2

Total number of correlations examined was 534 (89 taxa or indicators by six abiotic variables); regressions with more than one predictor were counted only once.

Table 6
Predictive capability of individual abiotic factors

Abiotic factor	No. of taxa or indicators	%
Dist to ocean	16	18.0
Dist to river	7	7.9
Depth	7	7.9
Mud fraction	5	5.6
Fetch	2	2.2
Current	0	0.0

Number of taxa or indicators for which significant relationships were found for each abiotic factor. Total n for each factor was 89 taxa or indicators. Some relationships are attributed to more than one factor.

side of Moreton Bay is essentially under ocean influence, it is of limited value for habitat mapping.

The generally poor predictive ability of abiotic variables shown in this study contrasts strongly with similar studies, albeit at a different scale. Zacharias et al. (1999) and Zacharias and Roff (2001) produced models based substantially and wholly (respectively) on abiotic variables that explained >70% of the pattern of intertidal diversity at the regional scale. In contrast, Schlacher et al. (1998) studied benthic community structure in a soft-sediment tropical lagoon at scales similar to the present study, and also found that sediment characteristics had only weak relationships with the distribution of biota.

The inability of the abiotic classification to predict patterns of biological similarity between sites accurately begs the question: do such patterns exist, or was the abiotic information unable to predict them because they were not there? The ordination analyses show clearly that patterns do exist, with strong and consistent groupings at solutions from three to six groups. This paper does not go into the nature of those groups in detail; that is the subject of another study. The inability of the abiotic data to predict such groups at this scale has implications for reserve planners and managers.

How broadly applicable is this finding? Compared to similar studies at other scales (Zacharias and Roff, 2001) the area encompassed by this study is more abiotically homogeneous, although major and obvious differences exist. Of particular note is that all the sampled sites are soft substrate, and all subtidal. Most abiotic habitat classification schemes (e.g. Marine Reserves Working Group, 2000 in Litt.) benefit from clear distinctions such as between soft and hard substrates, or coral versus rock versus gravel, and in these conditions abiotic variables can perform well in predicting patterns of biological similarity. At the other extreme, studies in soft sediment environments have found that a single environmental variable, e.g. current stress (Long et al., 1997) can predict distribution of epibenthos quite accurately in otherwise homogeneous situations.

This study falls between these two extremes but highlights the limitations of using abiotic surrogates for habitat mapping at the local scale. In this study, abiotic variables were not able to predict more subtle and complex patterns of biological distribution in a system that, although exclusively soft substrate, was quite variable in terms of depth, sediment composition and current velocity.

Factors other than those analysed in this study are clearly influencing biological distributions within the bay, and might be considered in three categories; unmeasured abiotic factors, ecological processes, and anthropogenic influences.

Could additional abiotic information have improved predictive capacity? Certainly, with additional datasets, it is possible that an abiotic classification could be constructed that would better predict the observed patterns of biological similarity. Much of the abiotic information found in previous studies to influence biological distributions operates at either very large (hundreds of kilometres, e.g. tidal range, salinity; Zacharias et al., 1999) or very small (tens of centimetres, e.g. topographic heterogeneity, Archambault and Bourget, 1996). To be of value in a study such as this, abiotic information must be available for all sites and be at scale that discriminates between sites. However, in order to provide abiotic

data detailed enough to model patterns of biological similarity, ground truthing would have to be so detailed one might as well survey the biota in the first place. For reserve planning, especially for considerations of representation, it is the biological distributions that are (or should be) the central interest.

There is a considerable volume of literature on the role of ecological processes in spatial variation in soft bottom ecosystems (e.g. Herman et al., 1999), although most studies are at finer scales than the current study, and focus more frequently on infauna than epifauna. Factors such as the timing and magnitude of recruitment (Olafsson et al., 1994; Fraschetti et al., 2003), the role of infauna in structuring sediment characteristics (e.g. Schaffner et al., 2001), effects of competition and predation (e.g. Beal et al., 2001), and the frequency and scale of disturbance (e.g. Cristoni et al., 2004) may all influence distributions of epibenthic organisms in Moreton Bay, but are outside the scope of this study. The finding that the abiotic variable Distance to Ocean was the single most influential variable in the present study (Table 6) indicates that processes relating to oceanic influences, as found by Udy and Dennison (1997) may be important.

Anthropogenic influences may also play an important role in biological distributions. Much work has been done on the influence of heavy metals (e.g. Stark et al., 2003), nutrients (e.g. Soltan et al., 2001), dredging (e.g. Poiner and Kennedy, 1984) and trawling (e.g. Engel and Kvitek, 1998) on benthic assemblages. The single largest point source for pollutants and nutrients in Moreton Bay is the Brisbane River. Costanzo et al. (2001), among others, have shown that the influence of the river rarely extends into the eastern part of the bay, although the abiotic variable Distance to River was equal second most influential in the present study (Table 6). Some dredging occurs in the eastern bay for sand extraction purposes (Dennison and Abal, 1999) but is very limited in relation to the size of the study area. Several types of fishery operate within the study area, including a benthic trawl fishery (Williams, 2002), which clearly has the potential to influence macrobenthic distributions. Most of the study area is potentially available to the fishery, although some parts are closed to trawling to protect seagrass beds, and others are not suitable or accessible due to shallow and mobile sand banks. In practice, less than a third of the study area is trawled. Whilst it may be an influence on biological distributions in the areas in which it occurs, published information on the distribution of effort and take in the fishery is not sufficiently detailed to allow any further discrimination between sites (Williams, 2002).

The above notwithstanding, this study set out to determine whether abiotic variables commonly used as surrogates could predict biological distributions with sufficient accuracy to be useful in designing marine protected areas for representation. Whilst a predictive capacity in the order of 30% indicates that the abiotic variables chosen have some relationship with the observed biological distributions, and may well play a role in structuring assemblages, the spatial analyses show that the errors of false homogeneity and false heterogeneity are high. A habitat map based on these available abiotic factors would be misleading, inaccurate and of little conservation value.

What does this mean for marine protected area planning? At the local scale, it is questionable whether habitat mapping, and resulting analyses of representation for use in marine protected area design, can be constructed with a reasonable degree of rigour from abiotic surrogates alone. Several authors have constructed classification schemes combining abiotic and biological information, often within nested scales (e.g. Connor et al., 1995). The subtext to these schemes seems to be that the abiotic information is necessary to supplement inadequate biological data. When biological data are not available, this is clearly necessary. The danger with this approach is that abiotic or hybrid classifications are then accepted as a basis for representation of patterns in biological distributions, without ever doing robust biological surveys at the appropriate scale. It is questionable, and certainly rarely tested, whether marine protected areas designed on this basis can have measurable benefits for conservation.

The performance of habitat classifications, whether based on abiotic information, purely biological data or a combination, is critically effected by the scale of mapping and the representation targets. Ward et al. (1999) constructed a site scale hybrid habitat classification of Jervis Bay on Australia's east coast which combined plant communities with depth, substrate type and physical features. This classification was found to perform better than separate classifications based on fish, invertebrate or plant assemblages at capturing species richness where 40% or more of each habitat type could be included in a simulated reserve. At lower representation targets (10% or 20%), a classification based on invertebrate assemblages was better than any other at capturing species richness. Direct comparisons with the present study cannot be drawn, since no purely abiotic habitat classification was tested by Ward et al. (1999), and the scale and area covered are both different by an order of magnitude. The Jervis Bay study also included substantial intertidal areas not considered in the present study.

It has been suggested (e.g. Stevens, 2002) that representation targets should be driven by conservation objectives, such as the capture of most (95%) of the known species richness within a given area. Ward et al. (1999) showed that for Jervis Bay, representation targets in the order of 80% would be required to achieve this, depending on the basis of the classification. The present

study does not attempt such an analysis, but this may be the basis of future work.

It is acknowledged that the biota captured in this survey does not constitute a comprehensive picture of Moreton Bay benthic biota. It is, of course, a relatively small subset of the total biota, in that it does not sample infauna, nekton or taxa smaller than the optical resolution of the sensor. All surveys capture subsets of the total biota, which are biological surrogates for biodiversity at scales from genes to ecosystems (Vanderklift et al., 1998; Ward et al., 1999), as are indicator groups proposed as tools for marine reserve selection (Gladstone, 2002). Such approaches are logically more robust that the use of abiotic surrogates if representation of patterns in biological distributions is the aim, but all require testing against other components of the total biota.

The survey component of this study was relatively quick and inexpensive, costing an order of magnitude less than a comparable diver based survey (one to two crew, a small outboard-powered vessel, 16 boat-days). The study has demonstrated that with off-the-shelf components and a little ingenuity, cost-effective surveys can be carried out over quite large areas at scales relevant to marine protected area design. The common perception that biological data (at an appropriate scale and in sufficient detail) for habitat mapping is not obtainable can be discarded in many cases.

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References

Agardy, T. (Ed.), 1995. The Science of Conservation in the Coastal Zone 1995. IUCN, Gland, Switzerland. 72pp.

Anon, 1997. Marine Park (Moreton Bay) Zoning Plan. Government Press, Office of the Queensland Parliamentary Counsel, Queensland, 103pp.

Archambault, P., Bourget, E., 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. Marine Ecology Progress Series 136, 111–121.

Barker, B.A., Helmond, I., Bax, N., Williams, A., Davenport, S., Wadley, V.A., 1999. Vessel-towed camera platform for sea-floor surveys of the continental shelf. Continental Shelf Research 19, 1161–1170.

Bax, N.J., Williams, A., 2001. Seabed Habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring. Marine and Freshwater Research 52, 491–512.

Beal, B.F., Parker, M.R., Vencile, K.W., 2001. Seasonal effects of intraspecific density and predator exclusion along a shore-level gradient on survival and growth of juveniles of the soft shell clam, *Mya arenaria* L., in Maine USA. Journal of Experimental Marine and Ecology 264, 133–169.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.

Connor, D.W., Hiscock, K., Foster-Smith, R.L., Covey, R., 1995. A classification system for benthic marine biotopes. In: Eleftheriou, A., Ansell, A.D., Smith, C.J. (Eds.), Biology and Ecology of Shallow Coastal Waters, European Biology Symposium, Hersonissos, Crete (Greece), 1993. Fredensborg – Denmark, Olsen and Olsen, pp. 155–166.

Costanzo, S.D., O'Donohue, M.J., Dennison, W.C., Longeran, N.R., Thomas, M., 2001. A new approach for detecting and mapping sewage impacts. Marine Pollution Bulletin 42 (2), 149–156.

Cristoni, C., Colangelo, M.A., Ceccherelli, V.U., 2004. Spatial scale and meiobenthic copepod recolonisation: testing the effect of disturbance size in a seagrass habitat. Journal of Experimental Marine Biology and Ecology 298, 49–70.

Davies, J., Foster-Smith, R.L., Sotheran, I.S., 1997. Marine biological mapping for environmental management using acoustic ground discrimination systems and geographic information systems. Underwater Technology 22, 167–172.

Dennison, W.C., Abal, E.G., 1999. Moreton Bay Study: a scientific basis for the healthy waterways campaign. South East Queensland Regional Water Quality Management Strategy/Brisbane City Council, Brisbane, Australia, 246pp.

Engel, J., Kvitek, R., 1998. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conservation Biology 12, 1204–1214.

Eyre, B., Hossain, S., McKee, L., 1998. A suspended sediment budget for the modified subtropical Brisbane River estuary, Australia. Estuarine, Coastal and Shelf Science 47, 513–522.

Fraschetti, S., Giangrande, A., Terlizzi, A., Boero, F., 2003. Pre- and post-settlement events in benthic community dynamics. Oceanologica Acta 25, 285–295.

Gabric, A.J., McEwan, J., Bell, P.R.F., 1998. Water quality and phytoplankton dynamics in Moreton Bay, south-eastern Queensland. I. Field survey and satellite data. Marine and Freshwater Research 49, 215–225.

Gladstone, W., 2002. The potential value of indicator groups in the selection of marine reserves. Biological Conservation 104, 211–220.

Herman, P.M.J., Middleburg, J.J., Van de Koppel, J., Heip, C.H.R., 1999. Ecology of estuarine macrobenthos. Advances in Ecological Research 29, 195–240.

Hockey, P.A.R., Branch, G.M., 1997. Criteria, objectives and methodology for evaluating marine protected areas in South Africa. In: Towards a New Policy on Marine Protected Areas for South Africa, Marine Reserves Task Group, South African Network for Coastal and Oceanic Research. Occasional Report No. 2, pp. 98–118.

Interim Marine and Coastal Regionalisation of Australia Technical Group, 1998. Interim Marine and Coastal Regionalisation for Australia: an ecosystem-based classification for marine and coastal environments. Version 3.3. Environment Australia, Commonwealth Department of the Environment, Canberra.

IUCN, 1994. Guidelines for Protected Area Management Categories, CNPPA with the Assistance of WCMC. IUCN, Gland, Switzerland and Cambridge, UK.

Kelleher, G., Bleakley C., Wells, S., 1995. A global representative system of marine protected areas: volumes I–IV. Great Barrier Reef Marine Park Authority, The World Bank, The World Conservation Union (IUCN).

Long, B.G., Bode, L., Mason L., Pitcher, C.R., 1997. Seabed current stress predicts the distribution and abundance of epibenthos in Torres Strait. Report to Australian Fisheries Management Authority, CSIRO, Australia.

Manly, B.F.J., 1997. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, London. 399pp.

O'Hara, T.D., 2001. Consistency of faunal and floral assemblages within temperate subtidal rocky reef habitats. Marine and Freshwater Research 52, 853–863.

Olafsson, E.B., Peterson, C.H., Ambrose Jr., W.G., 1994. Does recruitment limitation structure populations and communities in marine soft sediments: the relative significance of pre- and post-settlement processes? Oceanography and Marine Biology Annual Review 32, 65–109.

Poiner, I.R., Kennedy, R., 1984. Complex patterns of change in the macrobenthos of a large sandbank following dredging. 1. Community analysis. Marine Biology 78, 335–352.

Schaffner, L.C., Dellapenna, T.M., Hinchey, E.K., Friedrichs, C.T., Thompson Neubauer, M., Smith, M.E., Kuehl, S.A., 2001. Physical energy regimes, seabed dynamics, and organism-sediment interactions along an estuarine gradient. In: Aller, J.Y., Woodin, S.A., Aller, R.C. (Eds.), Organism–sediment interactions. University of South Carolina Press, Columbia, pp. 159–179.

Schlacher, T.A., Newell, P., Clavier, J., Schlacher-Hoenlinger, M.A., Chevillon, C., Britton, J., 1998. Soft-sediment benthic community structure in a coral reef lagoon – the prominence of spatial heterogeneity and 'spot endemism'. Marine Ecology Progress Series 174, 159–174.

Soltan, D., Verlaque, M., Boudouresque, C.F., Francour, P., 2001. Changes in macroalgal communities in the vicinity of a Mediterranean sewage outfall after the setting up of a treatment plant. Marine Pollution Bulletin 42, 59–70.

Stark, J.S., Riddle, M.J., Snape, I., Scouller, R.C., 2003. Human impacts in Antarctic marine soft sediment assemblages: correlations between multivariate biological patterns and environmental variables at Casey Station. Estuarine Coastal and Shelf Science 57, 717–734.

Stevens, T.F., 2002. Rigor and representativeness in marine protected area design. Coastal Management 30, 237–248.

Udy, J.W., Dennison, W.C., 1997. Physiological responses of seagrasses used to identify anthropogenic nutrient inputs. Marine and Freshwater Research 48, 605–614.

Vanderklift, M.A., Ward, T.J., Phillips, J.C., 1998. Use of assemblages derived from different taxonomic levels to select areas for conserving marine biodiversity. Biological Conservation 86, 307–315.

Ward, T.J., Vanderklift, M.A., Nicholls, A.O., Kenchington, R.A., 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. Ecological Applications 9, 691–698.

Williams, L.E. (Ed.), 2002. Queenslands fisheries resources: Current condition and recent trends 1988-2000. Queensland Fisheries Service Information Series QI02012, Department of Primary Industries, Brisbane, Australia.

Zacharias, M.A., Howes, D.E., 1998. An analysis of marine protected areas in British Columbia using a marine ecological classification. Natural Areas Journal 18 (1), 4–13.

Zacharias, M.A., Roff, J.C., 2001. Explanations of patterns of intertidal diversity at regional scales. Journal of Biogeography 28, 471–483.

Zacharias, M.A., Morris, M.C., Howes, D.E., 1999. Large scale characterization of intertidal communities using a predictive model. Journal of Experimental Marine Biology and Ecology 239, 223–242.