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A review of abiotic surrogates for marine benthic biodiversity

by

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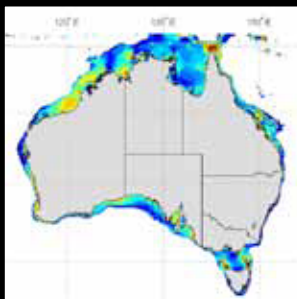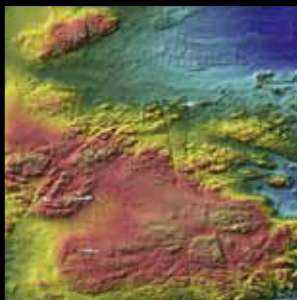
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MARINE BIODIVERSITY RESEARCH
Prediction and Management of Australia's Marine Biodiversity

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Executive Summary

A growing need to sustainably manage marine biodiversity at local, regional and global scales cannot be met by applying the limited existing biological data. Abiotic surrogates of biodiversity are thus increasingly valuable in filling the gaps in our knowledge of biodiversity patterns, especially identification of hotspots, habitats needed by endangered or commercially valuable species and systems or processes important to the sustained provision of ecosystem services. This review examines the use of abiotic variables as surrogates for patterns in benthic assemblages with particular regard to how variables are tied to processes affecting biodiversity and how easily those variables can be measured at scales relevant to resource management decisions.

Currents and wave action affect larval supply, food availability and disturbance regimes and can therefore be used to describe biodiversity patterns over local, regional and global scales. Direct gradient variables such as salinity, oxygen concentration and temperature can be strong predictive variables for larger systems, although local stability of water quality parameters may prevent usefulness of these factors at fine spatial scales.

Biological productivity has complex relationships with benthic biodiversity, and although the development of local and regional models cannot accurately predict outside the range of their biological sampling, remote sensing may provide necessary information. Indeed, interpolated values are available for much of the world's seas, and these are continually being refined by the collection of remote sensing and field data.

Sediment variables are often interconnected with complex relationships to biodiversity. The strength of the relationship between any one sediment variable and biodiversity may depend on the state of another sediment variable in that system. Percentage mud, percentage gravel, rugosity and compaction hold the strongest independent predictive power. Rugosity and the difference between gravel and finer sediments can be established using acoustic methods, but to quantify grain-size and measure compaction, a sample is necessary.

Pure spatial variables such as latitude, longitude and depth are not direct drivers of biodiversity patterns but often correspond with driving gradients that they can be of some use in prediction. In such cases it would be better to identify what the spatial variable is acting as a proxy for so boundaries for that variable are not overlooked. The utility of these potential surrogates will vary across spatial scales, quality of data, and management needs, and the continued focus on surrogate research will address the need of marine scientists and resource managers worldwide for accurate and robust predictions of species distribution patterns.

1. Introduction

Marine biodiversity is of direct benefit to society as a food source, potential pharmacopoeia (Hunt & Vincent 2006), stabilizer of inshore environments (Jie et al. 2001) and regulator of atmospheric processes (Murphy & Duffus 1996). Marine biodiversity provides indirect benefits to society through ecological stability (Menge et al. 1999) and benthic-pelagic coupling (Ponder et al. 2002) which contribute to self-sustaining marine ecosystems. Marine biodiversity also has recreational, aesthetic and intrinsic value (Ponder et al. 2002; Wilson 1994).

Describing marine biodiversity can be challenging, particularly for habitats with difficult-to-sample biota. Using the relationships between abiotic factors and biota to predict patterns of biodiversity offers a promising alternative to biological sampling. The idea that physical and chemical properties of a system can act as surrogates of biodiversity is intuitive, but it is only recently that the relationships between organisms and their environment have been studied in sufficient detail and tested with appropriate mathematical tools to allow estimates of biodiversity to be made based on environmental data alone (Meynard & Quinn 2007). Such surrogacy relationships can be based on physical or chemical properties of a habitat (abiotic surrogacy) or on a defined taxonomic group (biotic surrogacy).

The use of surrogates to assess diversity is particularly important if a natural resource management decision must be made based on minimal biological information. In the application of surrogacy to management questions, consideration must be given to the degree to which present-day benthic environments have been and will be impacted by human activities occurring over the last century. Benthic ecosystems have been negatively impacted by over-fishing (Jackson 2008), bottom trawling and dredging (Pauly et al. 2005), pollution of coastal waters (Halpern et al. 2008), aquaculture and introduced species (Galil 2000; Jackson 2008; Pauly et al. 2005) and human-induced climate change (Bindoff et al. 2007). The combination of these direct and indirect human impacts on the marine environment is inducing unprecedented changes in marine ecosystems, and further loss of biodiversity is likely (Jackson 2008). Logistical constraints may preclude biological sampling in some impacted or vulnerable areas, and abiotic surrogacy research may provide a viable means to estimate biodiversity for marine conservation and vulnerability assessment.

The aim of this review is to synthesize available information on benthic biodiversity and its measurement and to explore the function and utility of potential abiotic surrogates. The review is structured in three parts assessing the current status of surrogacy research and its importance to marine resource management. First, marine biodiversity is defined and its measurement discussed. Second, the roles of abiotic factors in shaping biodiversity are examined. Third, considerations relevant to surrogate utility are addressed.

One challenge facing marine scientists and resource managers is to make sufficiently accurate and robust predictions of biodiversity using the more extensive abiotic datasets currently available so those predictions can be applied to resource management strategies. Therefore, we also discuss the importance of surrogacy research to marine resource management.

2. Marine Biodiversity

Several levels of complexity can be examined when considering marine diversity. Genetic diversity within a species or population and diversity of functional roles within a community are informative variables to quantify (Gray 1997), but species is the unit of diversity most easily conceptualized and is therefore most commonly considered (Willig et al. 2003). Of the many definitions available, the most widely applied species model is that of a genetically distinct, reproductively isolated population (Mayr 1996). The number of species in a given space is often referred to as the species diversity but ecologists refer to this integer value as species "richness," denoted as S, reserving "diversity" for equation-derived values accounting for proportionality of species' populations (Magurran 2004).

Marine species range in size and complexity from viruses to whales (Snelgrove 2001), and a range of species compete for resources at each level of size and complexity. Bouchet (2006) reported 229 602 described marine species, but estimates of the grand total of marine taxa based on extrapolations from existing data vary widely: Grassle and Maciolek (1992) proposed that ten million species exist in the benthos alone, and May (1992) , using conservative assumptions, responded with an estimate of 500 000 benthic species. The range of these estimates indicate much work must be done to reliably estimate the existing richness of the world's seafloor and even then, describing the species would only be the first step in defining species' distributions, information critical to marine spatial planning.

2.1. Benthic Diversity at Different Scales

Because of the different sampling strategies required to account for diversity at different scales, ecologists divide animals of interest into non-taxonomic size groups: megafauna are large enough to identify by eye; macrofauna describes organisms small enough to require microscope attention for accurate identification and extends down to those retained on a 300 µm sieve; mieofauna pass through 300 µm mesh but are retained on a 44 µm sieve; and microbes (bacteria and protists) can pass through a 44 µm sieve. Microbes may represent the largest component of Earth's genetic diversity and biomass (Snelgrove 2001).

Each of these ecologically arbitrary size divisions generates a following among ecologists who tend to sample and model their component of interest as an independent unit, with communities therefore rarely treated holistically (Yeom & Adams 2007). As a result of this division of effort and thought, diversity measures for a given system may only take into account the community fraction of interest to the reporting specialist. This approach may ignore important processes at work on other scales (Ponder et al. 2002) but is often necessary to reduce the costs of sampling and processing.

New species of squid and whales are still being discovered (Chivian & Bernstein 2008) but, compared to megafauna, little is known about distributions and biology of most macrofaunal and meiofaunal species due to the difficulty of sampling and sorting material at these scales and the shortage of expert taxonomists (Bouchet 2006). Macrofauna and meiofauna are crucial components of the benthic ecosystem, playing key roles in nutrient cycling, benthic-pelagic coupling, bioturbation, and succession (Rex et al. 2006), and the response of these groups to environmental variables can be different to

that of the megafauna (Edgar 1999). Research on these groups tends to focus on the intertidal (Hourston et al. 2005) or very shallow systems (Dye 2005).

Finding a value for the species richness of an entire system is currently impossible as the shortage of taxonomic expertise and the large number of undescribed taxa preclude accurate identification of all organisms at all scales in all but the most intimately studied systems (Costello et al. 2006).

2.2. Biotic Data

There are five options for organism identification available to researchers undertaking surrogacy research: 1) Identify all organisms to the species level, 2) Identify subsets of taxa for which expertise is available to species level, 3) Identify species to a coarse taxonomic level, 4) Identify target species, or 5) Identify functional groups. Biological surrogacy, where the presence of one taxon implies the presence of others is not addressed here. As species is the level at which organisms react to their habitat (Bertrand et al. 2006), the first option is the most comprehensive and will have the greatest power to detect relationships with abiotic variables. Unfortunately, identification to species level is often difficult, time-consuming and costly (Ponder et al. 2002). Use of coarse taxonomic resolution may hinder the quantification of biodiversity and the utility of potential surrogates (Bertrand et al. 2006) and spatial variation becomes less distinct as taxonomic resolution is lowered (Anderson et al. 2005). Several studies have shown that identification at the genus-, family-, and even order-level is sufficient to detect community response to environmental gradients (Wlodarska-Kowalczuk & Kedra 2007). Nevertheless, even at genus level there may be sufficient biological disparity between closely related organisms to dictate contrasting distributions that limit the utility of surrogates based on taxonomic generalizations (Pitcher et al. 2007).The effectiveness of target species analysis depends on the group chosen (Wlodarska-Kowalczuk & Kedra 2007), and the utility of target groups may vary according to the age of a community (Magierowski & Johnson 2006).

The final approach to quantifying diversity involves identifying organism roles within a system. Functional groups describe organisms that share a similar physiological or ecological function e.g.: deposit feeders, bioturbators, predators (Bonsdorff & Pearson 1999). When clearly defined, such groupings can be used as a proxy for diversity and may provide a more practical way to assess potential surrogacy relationships than strict taxonomic approaches because biological function is more closely associated with abiotic variables than taxonomy. The validity of using functional groups has been questioned because analyses based on such divisions may be meaningless without more comprehensive knowledge about life history and biology of marine biota than is currently available for most species (Pearson 2001). In addition, some evidence points to species identity being closely linked to ecosystem services such as bioturbation (Norling et al. 2007). Potential surrogacy relationships may best be examined by incorporating multiple functions related to the environmental variable of interest, particularly for soft sediment communities (Pearson 2001). The choice of functional group divisions will affect interpretation of biodiversity patterns, as well as the magnitude and significance of relationships between abiotic variables and biota (Sanders et al. 2007).

Further investigation into the effects of taxonomic resolution on the ability to detect patterns is needed as they likely vary across ecosystems and communities. The utility of functional groups to surrogacy has not been examined, and future research

should investigate the suitability of functional group perspectives in the development of predictive models of ecological and biological function based on abiotic factors (Sanders et al. 2007).

2.3. Diversity Indices

Species richness, also referred to as alpha diversity, increases monotonically with the area or volume sampled (He & Legendre 2002) and with sampling effort (Benkendorff & Davis 2002). Therefore, when sampling effort is even, comparison of the number of species (richness) should be a valid way to assess biological response to impacts or environmental differences between sites. Different species rarely occur in equal numbers at a site, and the proportion that each species contributes to the community can be as important in defining differences between systems as species richness may be more sensitive to environmental change (Gray 1997). Diversity indices seek to turn the number of species and the proportionality of their relative counts in a given area into a single number for ready comparison of samples, sites or ecosystems (Magurran 2004). This often transforms the relatively simple integers of species richness into complex representations of proportionality. Most proportionality-based diversity indices are geared to record a high number in assemblages where a large number of species occur in similar numbers (high evenness) and a low number if a small number of species dominate a sample or system (low evenness) (Magurran 2004).

Sampling cannot be expected to account for every species in every assemblage (Chao et al. 2005). Richness estimators calculate the number of species expected based on the sequence in which they are encountered in a series of samples, using random iterations of sample data through equations that account for richness and proportionality. Richness estimators are used to determine how many species might be expected in an assemblage under differing levels of sampling (Ugland et al. 2003).

The change in species richness along environmental gradients is referred to as beta diversity. Low beta values indicate assemblage equivalency, and high values indicate assemblage disparity (Magurran 2004). Simple measures of beta diversity compare alpha diversity against the species richness of a region (gamma diversity) (Magurran 2004). Others make direct comparisons of species' presence and absence (e.g. Jaccard's coefficient) or species' relative proportions (e.g. Bray-Curtis coefficient) between two systems (Clarke & Warwick 1998).

The values incorporated by diversity and evenness measures only take into account the number of species and their proportions. Patterns described by these indices may be of interest in an environmental impact assessment, but interpretation of the results back to ecological processes is difficult (Clarke & Warwick 2001). An increase in species richness or evenness can be expected immediately after environmental change when resources, previously fully utilized, are suddenly made available to recruiting species and pre-climax community structures (Connell 1978). Therefore, it is difficult to define ecological change at intermediate levels of disturbance or to examine biological responses to natural environmental gradients using diversity information alone (Clarke & Gorley 2006).

Diversity indices can act as tools to identify community change in response to environmental change, or habitat gradients and richness estimates derived from iterative processes can be used to explore assemblage differences graphically through rarefaction curves. Diversity indices may suggest new avenues of investigation, but the index most

appropriate to a particular situation must be chosen and the resulting values considered carefully with regard for the environmental drivers of a system and how that index will account for them (Magurran 2004). As the values generated by many diversity and evenness indices are complex, mathematical representations of integer data usually cannot be used in hypothesis testing (Legendre & Legendre 1998).

3.   Patterns of Benthic Diversity and Their Drivers

The goal of surrogacy research is to determine which easily measured characteristics best describe the species assemblage of a particular space and time (Moore et al. 1991). These characteristics are then expected to act as predictors of species assemblages in unexplored areas (Franklin 1995). Pitcher (2007) identified grain size, carbonate composition, available space, benthic irradiance, sheer stress, bathymetry, bottom water physical properties, nutrient concentrations and turbidity as abiotic surrogates of biotic distributions on the Great Barrier Reef; but these variables, while useful predictors, may not be the forces driving the patterns they describe.

The influence of abiotic factors on species assemblages is due to the effect they exert on fundamental niches. A species' fundamental niche was defined by Austin *et al.* (1990) as "that hypervolume defined by environmental dimensions within which a species can survive and reproduce." Fundamental niches are rarely fully realized by species because interspecific competition, disease and disturbance events displace individuals and populations, resulting in a reduced occupied hypervolume, often referred to as the realised niche (Austin & Smith 1989). The environmental gradients that describe a species' fundamental niche can be broadly grouped into resource gradients – e.g. chemicals or energy consumed by a species; direct gradients – variables with a physiological influence on a species but not consumed by it – e.g. sediment grain size or temperature; and indirect gradients – variables correlated with direct and resource gradients but with no physiological connection to the species – e.g. depth and latitude (Meynard & Quinn 2007). When niche theory was first proposed, species were expected to exhibit a Gaussian distribution to environmental gradients but skewed distributions are more common in ecological studies as the effects of additional variables express their influence (Karadzic et al. 2003).

Predictions of biodiversity can also be made using neutral theory, an idea with similarities to island biogeography theory (Volkov et al. 2003), in which relative species abundances are assumed to be determined by random immigration to a system (Leigh Jr 2007). Neutral theory is not universal (Leigh Jr 2007) and has been shown to conflict with some empirical data (Dornelas et al. 2006; McGill 2003), thus niche theory remains the most appropriate ecological model on which to base surrogacy research.

The abiotic variables historically ascribed the greatest direct influence over benthic organism distributions are temperature, salinity, oxygen concentration, light availability and sediment composition (Snelgrove 2001). A model of these influences and some of their potential synergies is given in Figure 1, and a range of recent studies that have quantified the extent to which abiotic information accounted for biotic data are noted in Table 3.1. Olabarria (2006) found depth accounted for as much as a quarter of the

variance in benthic diversity in deep systems but, as benthic organisms lack an apparent mechanism for measuring depth, some correlated water quality parameter or seafloor characteristic most likely influences the settlement, recruitment and survival processes that result in the observed depth related patterns. In the same sense, latitude can act as a proxy for a range of gradients of direct importance to benthic organisms regardless of their actual position relative to the equator. Indirect gradients can be location specific, giving them limited value in explaining realised niches (Austin & Smith 1989) but if the correlation between the indirect and the direct drivers are general enough, predictions based on the indirect variables are of value (Moore et al. 1991), particularly when they are easily measured.

Gray (2002) reduced Snelgrove's list of direct drivers (2001) to productivity, temperature and sediment composition as the dominant variables in determining regional benthic richness, noting that temperature and productivity are often correlated to depth and latitude. Combinations of these driving influences occur with varying spatial and temporal consistency, in turn producing semi-regular patterns of biodiversity. The validity and origin of several identified general benthic biodiversity patterns are the focus of much recent debate. For example, the latitudinal richness gradient, widely accepted as a rule for benthic fauna since the mid twentieth century (Thorson 1957) has recently been shown to be weaker than previously thought (Snelgrove 2001) or entirely incorrect for some taxa or systems (Rex et al. 2005).
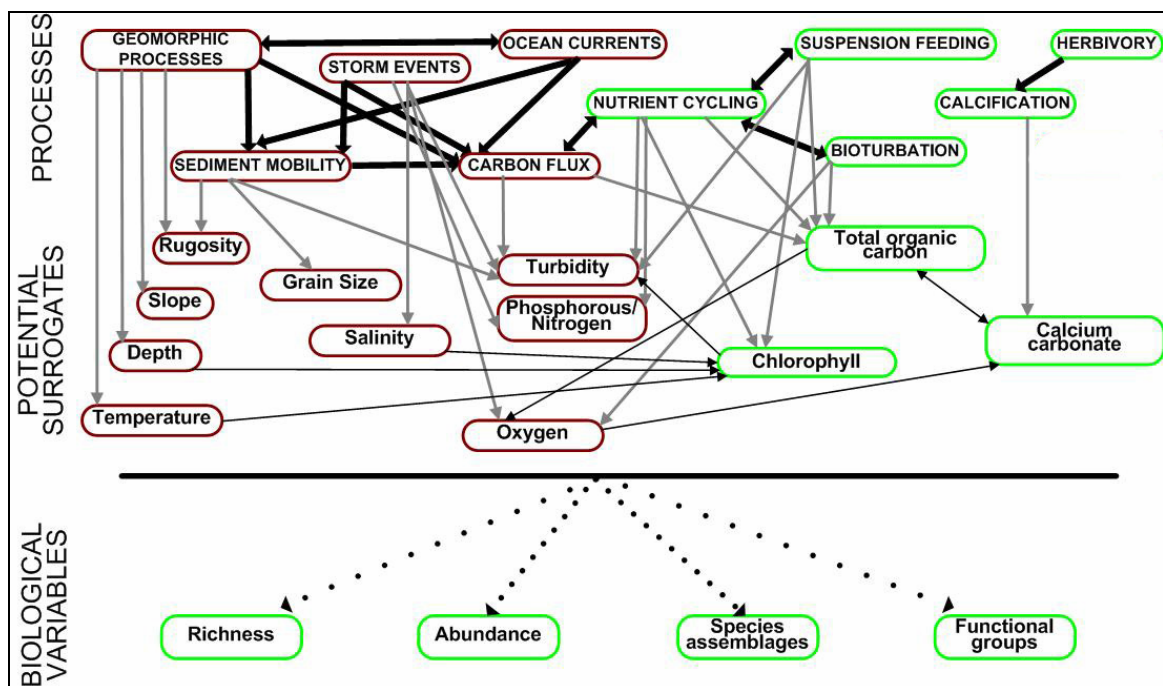
Figure 3.1. Conceptual map of the drivers of biodiversity in marine systems and some potential surrogates. Black lines indicate relationships between potential surrogates. Bold black lines represent relationships between processes. Gray lines show potential surrogates linked to a process. Dotted lines show potential relationships between surrogates and biological variables. Brown borders enclose abiotic factors. Green borders enclose biological or biophysical factors.

Table 3.1. Key results of surrogacy studies in which species assembly was analysed against abiotic variables.

Study	Important/best variables	% variability accounted for	Statistical process
(Post et al. 2006)	% mud, % gravel, disturbance, depth	59	BIOENV
(Passlow et al. 2006)	depth, longitude	25	BIOENV
(Sanders et al. 2007)	depth	65	BIOENV
(Beaman et al. 2005)	Slope, % gravel, %CaCo$_3$	75	BIOENV
(Beaman & Harris 2007)	Slope, % gravel, turbidity	62	BIOENV
(Williams et al. 2006)	Depth, latitude, gear type, longitude	44	BIOENV
(Stevens & Connolly 2004)	% mud, distance to ocean	30	Spearmans
(Ellingsen et al. 2005)	Depth, depth	29	Linear regression
(Gogina et al. 2010)	Depth, total organic content	50, 43	BIOENV (also Spearmans, CCA)

3.1. Spatial Variables

Although pure spatial variables are not the driving force behind the patterns they can be used to describe, variables such as latitude, longitude and depth can act as strong proxies for factors that influence species richness such as temperature, day length, light penetration and a variety of dispersal variables (Hawkins 2001).

3.1.1. Latitude

Increasing species richness with increasing proximity to the equator is a long recognised biogeographic pattern (Cox & Moore 2005). While this pattern has been documented in the marine environment (Attrill et al. 2001) it has recently been found to be less general than previously thought (Gray 2001). The terrestrial latitudinal richness gradient, first recorded by von Humboldt at the start of the nineteenth century (Willig et al. 2003) and noted by Darwin on the Beagle (Darwin 1839), led researchers to seek matching patterns in marine systems (Stehli et al. 1967). Particularly strong latitudinal signals are evident in the molluscan fauna on the coastal shelves of North America (Gage 1996) and among deep sea macrofauna (Piepenburg et al. 2002).

Hawkins (2003) and Willig (2003) each cite thirty hypotheses to explain latitudinal richness gradients. These were categorised by Mittelbach (2007) into ecological, historical and evolutionary groups. The ecological hypotheses concentrate on the different adaptive challenges faced by organisms living in different climatic zones: polar and temperate organisms must adapt to environmental conditions (Schemske 2002) while tropical organisms, dealing with less harsh abiotic extremes, adapt to biotic interactions (Crame 2000). Historical explanations concentrate on the age and stability of richness hotspots (Alongi 1990). There is evidence that modern benthic taxa have their origins in the ancient Tethys Sea, radiating into temperate and polar regions during the Miocene (Gage 2004). Evolutionary models incorporate several possible drivers for high rates of speciation including the wide variety of microhabitats available in tropical regions (Rex et al. 2005) and higher rates of molecular evolution (Kerswell 2006).

Attempts to measure and explain the extent of a latitudinal richness gradient in taxa other than molluscs on broad geographic scales have found less evidence for a marine equivalent to the terrestrial pattern (Gray 2001) and brought into question the treatment of data in describing such patterns. For example, Thorson's (1956) pattern of increasing richness in benthic epifauna toward the equator was based only on the 140,000 marine taxa known at the time (Snelgrove 2001).

In contrast to the northern hemisphere, southern hemisphere faunal richness does not show clear latitudinal gradients. Surveys of Antarctic fauna reveal a much higher richness among animals than the depauperate arctic (Brey et al. 1994). Some taxa actually become more specious towards the poles, and the Latitudinal Gradient Project has been established to examine ecological patterns in a range of systems using latitude as a surrogate for climatic variables in the Ross Sea (Howard-Williams et al. 2006). The age and stability of Antarctic shelf benthos may be a potential contributor to local high species richness (Gray 2002). Box-core sampling of isopods on Australia's south-east slope (Poore et al. 1994) and fish trawls on the south-west slope (Williams & Bax 2001) provide estimates of species and family richness much higher than those of equivalent mid-latitude regions in the northern hemisphere.

Peak richness among bryozoans and some groups of crustaceans occur in the temperate southern latitudes (Barnard 1991; Barnes & Griffiths 2008; Bolton 1996; Kerswell 2006); marine macro-algae and their associated faunal communities, confined to shallow waters, exhibit a bimodal relationship with latitude. Algal richness hotspots occur in both northern and southern temperate regions (Fraser & Currie 1996). This could be due to depressed tropical algal richness caused by direct competition between algae and corals (Snelgrove 2001), but Kerswell (2006) sought a driving mechanism in oceanic currents which, due to their relative direction of rotation in the northern and southern hemispheres, may promote algal propagule dispersal from tropical to temperate regions.

Diversity responses to pure spatial gradients can vary depending on how assemblage data are treated. Ellingsen (2005) determined that latitude could account for variance in richness of molluscs (11.8 % explained), annelids (9.6 %) and crustaceans (13.7 %) in Norwegian shelf benthos, but this influence dropped (4.9 %) when assemblages were considered collectively.

3.1.2. Longitude

Although less dramatic than the latitudinal changes in species richness, longitudinal diversity gradients are also evident, and richness hotspots occur in the western regions of both the Pacific and the Atlantic (Jones 1950). The Australasian tropical systems are particularly species rich because of their proximity to the highly diverse Indo-West Pacific region. Coral diversity decreases as one moves eastwards or westwards away from the Indo-West Pacific (Veron 1995). Similar patterns have been found in the cool temperate oceans where bryozoans decrease in diversity away from an Australasian hotspot (Barnes & Griffiths 2008). While significant species turnover (high beta diversity) was measured across the southern Australian coastline, echinoderm and decapod species richness did not vary significantly with longitude (O'Hara & Poore 2000). Kerswell (2006) attributes the algal component of longitudinal richness patterns to propagule distribution caused by oceanic currents, in this case carrying material westward either side of the equator with no equivalent mechanism for eastward dispersal at that latitude.

At a local scale (1-2°) the effects of latitude or longitude on patterns of biodiversity will likely not be observable (Coleman et al. 2007). When observed at local scales, continental patterns are disrupted by other spatial variables (e.g. depth) and environmental ones (e.g. substrate), but general spatial patterns are useful as surrogates of benthic biodiversity at a global scale.

3.1.3. Depth

Depth has been a consistently powerful explanatory variable in benthic studies (Nicolaidou & Papadopoulou 1989, Gogina et al. 2010). When generalising from shallow to deep, intertidal and estuarine systems exhibit high biomass and low species richness caused by high productivity and extreme environmental conditions (Edgar 2001), coastal shelves have moderate biomass and species richness (Snelgrove 2001), and the deep sea shows a decrease in biomass and increase in richness (Levin et al. 2001). Peak benthic species richness values have been recorded seaward of the continental rise, excluding the deep sea (Snelgrove 2001). The lower slope and abyssal plains become comparatively depauperate for some groups, and species turnover tends to be high (Paterson et al. 1992). Levin et al. (2001) stated that the deep sea houses greater diversity than coastal shelf systems, although at far lower abundances. Areas with low abundance and high species turnover require greater sampling effort to reliably account for diversity (Etter & Mullineaux 2001).

High relief benthic habitats offer refuge from predators and settlement surfaces not available on flat bottoms. Seagrass beds, reefs, mangrove forests and algal assemblages are home to more species than the adjacent sandy or muddy substrate, accounting for increased richness at a local and regional scale. Seagrasses are poor as a source of food for grazing taxa (Fry 2006), but the vertical structure provided by plants offer habitat for edible epiphytes in addition to being a refuge from predation (Jenkins & Wheatley 1998). Biogenic structures such as worm tubes, mussel beds and hard coral skeletons offer similar habitat advantages (Callaway 2006; Nakamura & Sano 2005; Reise 1981; Tsuchiya & Nishihira 1986).

3.2. Seabed Substrate Parameters

3.2.1. General Properties of Substrate Types

Numerous studies have provided evidence to show significant differences in the species composition between 'hard' and 'soft' substrata (Beaman et al. 2005; Beaman & Harris 2007; Williams & Bax 2001). For practical purposes, 'soft substrate' is usually defined as detrital mineral or biogenic sediment comprising grains with a mean diameter less than 2 mm, although gravel size fractions are often included (Lewis & McConchie 1994). The term 'hard substrate' is typically used to represent rock outcrops but may include sediments with large grain size (e.g. cobbles, boulders) since these materials can provide a surface that is functionally comparable to bedrock. While the contrast between soft and hard substratum is conceptually simple, defining the boundary between soft and hard substrates can be complex in practice because some rock types are friable or semi-consolidated and may be partly covered by sediment (Ryan et al. 2007b). In addition, because the boundaries between adjacent soft-sediment environments are not always as sharp as those across hard and soft substrate features, the associated boundaries between

biological assemblages may be gradational and spatially complex (Beaman & Harris 2007).

Sediment particle size distribution and composition on the seabed express a strong influence on the morphology and life history of species living in soft sediments (Jones 1950). These variables are determined by complex interactions between local geology, rates of sediment production and supply, actions of bioeroders, current and wave induced bed stress, and slope (Reineck & Singh 1980). Generally, in high-energy areas, coarse sediments (gravel) will predominate, whereas lower energy (depositional) areas are muddy, although there are exceptions (Foster 2001; Hart & Kench 2007; Rees et al. 2007) which have led to a highly complex and variable distribution of seabed sediment types on the shelf and slope.

Although several sediment surrogacy relationships are well documented (Beaman & Harris 2007; Brown et al. 2001; Degraer et al. 2008), the nature and strength of sedimentary surrogates for species composition within soft sediment environments remains a subject of debate (Dye 2006; Inoue et al. 2008; Stevens & Connolly 2004). Soft substrates are home to epifauna and infauna and plant life may include seagrasses (and their epiphytes) or microphytic algae occurring at the sediment-water interface. Hard substrates can act as habitat for epifauna and encrusting or macro-algae, but infauna are excluded.

Many apparent relationships between sediment type and biota remain untested in an experimental sense (Whitlatch 1981) and have been challenged (Snelgrove & Butman 1994). Table 3.2 collates information on the properties of soft-sediment benthic substrates that appear to influence distributions of benthic organisms. More detailed examinations of the relationships between these variables and the biota will follow.

Table 3.2. Soft sediment variables considered as potential abiotic surrogates of benthic biodiversity.

Parameter	Surrogacy potential	Mechanism	Ease of measurement	Source
Mean grain size	Poor in poorly sorted sediments	N/A – indirect gradient variable.	Needs physical sample. Processing becoming faster with automation.	(Degraer et al. 2008; Diaz et al. 2004)
% mud	Strong	Provides habitat or food for infauna.	As per mean grain size.	(Degraer et al. 2008; Diaz et al. 2004)
% sand	Poor on its own, tends to be inverse to mud	Provides habitat or food for infauna and foraging animals. High permeability offers opportunity for oxygenation of lower horizons.	As per mean grain size.	(Snelgrove & Butman 1994)
% gravel	Strong	Acts as a settlement surface and likely to have large interstices to act as habitat for cryptic species.	Can be differentiated from sand and mud by acoustic means.	(Kostylev et al. 2001)
Sorting	Not established but potentially valuable	Contributes to size of interstices.	As per mean grain size.	(Whitlach 1981)
Skewness	Noted but not quantified	Increased food availability with positive skewness.	As per mean grain size.	(Hogue & Miller 1981)
Compaction/ Porosity	Strong	Contributes to size of interstices.	Requires careful treatment of an undisturbed sample. Cannot be determined from stored material.	(Degraer et al. 2008; Edgar 2001)
Rugosity	Strong	Disturbance in unstable sediments (dunes, ripples, bedforms) depresses richness and biomass. These features may also affect settlement by changing circulation patterns.	Can be identified using acoustic means.	(Kostylev et al. 2001; Thouzeau et al. 1991)

3.2.2. Grain Size and Size Variation

Quantitative measures of sediment grain size (e.g. percentage mud, mean grain size) have often been linked to the distribution of infaunal and epifaunal benthic communities (Degraer et al. 2008; Whitlach 1981) (Table 3.3). Research conducted between the 1950s and 1990s concluded that seabed grain-size, measured from grab or dredge samples, exerts strong control on the distribution of benthic assemblages (Ellingsen & Gray 2002; Etter & Grassle 1992; Gray 1974; Rhoads 1974; Sanders 1958; Snelgrove & Butman 1994; Whitlach 1981). Clear influences have been indicated between sediment infauna (meio- and macrofauna) and the physical structure of sediment such as grain-size parameters and the level of sediment compaction (Degraer et al. 2008; Edgar 2001). The influence of grain size properties on epifaunal or demersal species distributions is clear in some environments (Greene et al. 2007a) but is likely to be one of several physical factors, such as seabed sediment mobility, deposit-feeding potential, turbidity and the potential for attachment, that are important driving factors (Snelgrove & Butman 1994).

Table 3.3. Faunal size classification and qualitative 'soft sediment' relationships after (Edgar 2001).

Classification	Faunal type	Minimum sediment size class	Example faunal groups
Megafauna (> 10 mm)	Epifauna	n/a	Flatfish, gobies, flatheads, dragonets, stingrays, shrimp, holothurians, heart urchins, brittle stars, various crabs.
Macrofauna (0.5-10 mm)	Infauna, epifauna	Very coarse sand	Amphipods, callianassid shrimps, bivalves, polychaetes
Meiofauna (0.063-0.5 mm)	Infauna	Fine sand	Nematodes, harpacticoid copepods, flatworms
Microfauna (< 0.063 mm)	Infauna	Silt, clay	Protozoa, bacteria, fungi

Several summary statistics are derived from standardised techniques that measure the range and abundance of sediment grain size in a sample, including mean grain size, standard deviation of the size range around the mean (sorting) and the symmetry or preferential spread (skewness) to one side of the mean (Blott & Pye 2001).

Mean grain size measurements alone do not take into account particle size variation (sediment sorting) or particle shape (e.g. disc or rod), and are therefore most useful for describing highly unimodal sediment grain size distributions (Lewis & McConchie 1994). Direct comparison of mean grain size may be misleading as a poorly sorted sediment of mud and gravel could produce the same value as a well sorted sand despite representing an entirely different habitat. The mean grain size value is the most commonly reported measure of sediment physical properties because it is relatively easy to measure and it is conceptually simple to represent a sample with one value that captures a basic seabed property, but the information lost in generating the mean may decrease its potential as a biodiversity surrogate (Snelgrove & Butman 1994).

Sorting, the standard deviation of grain size distribution, is a potentially valuable surrogate because it indicates the amount of interstitial space available within a sediment for benthic organisms to use as habitat (Gray 1974). For example, sedimentary environments that are poorly sorted, such as cobble and boulder fields, may incorporate several orders of magnitude difference in sediment grain size, forming complex three dimensional benthichabitat (Motta et al. 2003). Grain size range also determines the

amount of space between particles. In heterogenous sediments, interstices between large particles may be completely filled with smaller grains.

Despite the potential for sorting as a habitat indicator, Whitlach (1981) could not establish any correlation between sediment sorting and species diversity in benthic deposit feeders in a study of animal-sediment patterns in an intertidal setting. Sorting remains a parameter that few studies have considered in the context of the potential for explaining infaunal or epifaunal distribution patterns.

The skewness of a grain size distribution is rarely reported in studies of soft-sediment benthic habitats. The utility of this parameter lies in it being a measure of the tail, or extremes, of the grain size distribution. A distribution with strong positive skewness (+1 to +3) has an excess of fine-grained particles relative to a normal distribution with the same mean and strong negative skewness (-3 to -1) reflects an excess of coarse grains (Folk 1974). In the case of a positively skewed distribution for sand-dominated sediment, the fine fraction may include sediment of organic origin that could represent an important food source for infauna. This was observed (but not quantified) by Hogue and Miller (1981) in the shallow subsurface of sand ripples where silt represents a potential food source for nematodes.

3.2.3. Gravel

Sediments dominated by size fractions greater than 2 mm are classed as 'gravel,' incorporating granules (2 - 4 mm), pebbles (4 - 64 mm), cobbles (64 - 256 mm) and boulders (> 256 mm) (Wentworth 1922). These deposits have the greatest degree of three dimensional structure, permeability and the largest interstitial spaces offering shelter from predators and strong currents. In the English Channel, Brown et al. (2001) found presence or absence of gravel to be the most important variable influencing community composition. On Georges Bank in the northwest Atlantic, Thouzeau (1991) found significant changes in species richness, total abundance and biomass with differing sediment type, with higher values being associated with gravel substrates. Kostylev *et al.* (2001) also recognised the importance of gravel lags on the Scotian Shelf and subsequently identified strong links to scallop distribution and stock abundance, readily defined by high acoustic backscatter (Kostylev et al. 2003). Hard substrate fauna may recruit to sparsely scattered cobbles or shell debris large and stable enough to be suitable for permanent colonisation (Auster & Langton 1999). Very coarse sediments are generally acoustically distinct from finer material (e.g. muds and sands) and are readily mapped by acoustic mechanisms (Kostylev et al. 2003).

3.2.3.1 Boulders and Cobbles

Boulder fields are characterised by high densities of organisms due to their provision of refuge at a range of scales and possibly due to their effects on local hydrodynamics and grain size (Smith & Otway 1997). Boulders provide a complex microhabitat comprising upper surfaces (dominated by algae and providing demersal fish habitat), lower surfaces (dominated by sponges, bryozoans and ascidians), and soft sediment habitats beneath (Motta et al. 2003). The large interstices provided by semi-stationary boulders have been shown to be important sheltering and aggregation sites for numerous fish (Greene et al. 2007a) which use boulders to feed from and as a shelter from predators. Certain species also use the sheltered undersides of boulders to deposit egg masses (e.g. gastropods in

Przeslawski & Davis 2007), thereby making boulders important in reproduction and larval recruitment. Boulder and cobble aggregations also provide significant interstitial habitat for a range of crypto-benthic communities (Patzner 1999). Motta et al. (2003) showed that the sediments underneath boulders were affected by complex hydrodynamic conditions, and incorporate a high percentage of organic matter even in relatively coarse sediments, such as gravel, where levels of organic material are often thought to be low.

Cobble-dominated sediments are typically undisturbed by fair-weather wave-generated currents and most tidal currents. Consequently, these sediments are functionally similar to 'hard' substrate in that they are available for colonisation by attaching organisms (Brown et al. 2001) and also provide cryptic shelter; however, they may be periodically mobilised by storms (Lindholm et al. 2001).

3.2.3.2 Granules and Pebbles

Granule to pebble-sized deposits comprise rock fragments or biogenic calcium carbonate and are often hydrodynamically mobilised. These finer-grained gravels provide important continental shelf habitats that influence the distribution of a range of benthic biota (Beaman et al. 2005). As with larger-grain material, granules and pebbles form a highly permeable substrate with interstitial cavities and 3D-microstructure that is large enough to host a range of infauna, depending on the degree of sediment sorting.

Some organisms (molluscs, corals, green and red calcareous algae) generate gravel-fraction material through the production of calcareous skeletons. In areas of high calcium fixation these organisms contribute to the formation of a gravel-dominated habitat such that a measure of carbonate gravel is a potentially valuable surrogate for some benthic communities. Granule to cobble-sized coral rubble and shingle are important habitats which influence larval settlement on and adjacent to coral reefs (Mumby & Harborne 1999). Similarly, rhodolith beds are recognised as habitat with high local infaunal and epifaunal biodiversity (Hinojosa-Arango & Riosmena-Rodriguez 2004) where faunal settlement is enhanced (Culliney 1974) and three-dimensional microhabitats exist for many surficial organisms (Foster 2001). While high gravel proportion can act as a useful abiotic surrogate (Auster & Langton 1999; Greene et al. 1995; Kostylev et al. 2001; Thouzeau et al. 1991), small gravel percentages in otherwise sandy or muddy samples appear to have little bearing on biodiversity patterns (Post et al. 2006).

3.2.4. Sand and Mud

Sandy habitat is a widely recognised term used to describe expanses of relatively bare (devoid of obvious epifauna) sediment, mainly quartz or carbonate, comprising grains that range from 63 µm to 2 mm, featuring variable sediment sorting properties and often characterised by ripple or dune bedforms (Ryan et al. 2007a). Sand dominated sediments are easily mobilised as bedload in moderate to high energy continental shelf settings, resulting in the development of a dynamic bedform dominated seafloor (Hemer 2006). Large epibenthic and demersal species tend to occur in low abundance or as ephemeral visitors, a feature attributable to the absence of shelter, high sediment mobility, and lack of a firm substrate for use by attaching organisms (Gray 1974). Sandy habitats are important for burrowing organisms and their predators and provide foraging areas for species which may also use nearby firm substrate areas for sheltering purposes (Ross et al. 2007). The bulk of macrofaunal biomass and richness is concentrated in the first few

centimeters of soft sediments (Snelgrove 2001). Below this, oxygen penetration is matched by oxygen consumption, and organisms must be able to use anaerobic respiration or maintain a link to the oxygenated water above to survive (Snelgrove & Butman 1994). Large, loosely packed particles offer greater oxygen penetration than fine, dense muds.

Mud comprises grains including silt (4 µm – 63 µm) and clay (<4 µm) (Wentworth 1922). The term often has compositional connotations implying a soft often dark sediment which may contain detrital minerals and have a high organic content (Rhoads 1974). Silty muds resuspend easily and do not aggregate into bedforms such as ripples and dunes (Hemer 2006), although biogenic microstructures may be common (e.g. burrow holes, mounds, traces). Fine muds (clay) can be strongly cohesive due to electrostatic bonds between clay particles, which can make them more resistant to resuspension (Lewis & McConchie 1994).

The high particle surface area to volume ratios available in muddy sediments offer deposit feeders optimal feeding (Taghon 1988). Coarse sediments generated by the removal of fine material by currents offer similar advantages to suspension feeders as food bearing currents are more likely to support their survival (Wildish & Kristmanson 1997). Thus, a measure of percentage volume sand content can offer reciprocal surrogacy value to percentage mud, where gravel proportions are low. Functional associations can be blurred, however, where the grouping of organisms as suspension or deposit feeders is unclear. Whitlach (1981) also noted that intuitive ideas about recruitment to muddy and sandy sediments were confounded by high numbers of deposit and suspension feeding taxa co-occurring in some soft sediments.

Few studies identify percentage sand as a stronger influence on the distribution of benthic communities than percentage mud or gravel so it is likely that sand percentage alone is a relatively poor surrogate (i.e. the difference between mud or gravel and sand is less than the difference between unconsolidated and consolidated sediment). This is a point strongly argued by Snelgrove and Butman (1994) who recognised the importance of looking beyond grain size patterns to also consider sediment dynamics and hydrodynamics in determining organism distributions.

A range of benthic assemblages can occur on sandy or muddy substrates in a small area indicating the significant influence of other physical variables, especially hydrodynamics, in defining community structure (Wildish & Kristmanson 1997). Recent studies have found that the relationship between muddy substrates and benthic taxa appears varied and complex. In the English Channel a combination of factors including mud content and hydrodynamic forces correlated with species distributions in coarse and muddy sediments (Freeman & Rogers 2003). Similarly, in the Arctic, an association of muddy sediments and high total organic carbon content was recognised as an important environmental control on the distribution of macrofaunal communities, particularly in open-sea environments (Denisenko et al. 2003). In contrast, Post et al. (2006) found relatively weak links between mud content and the density of taxa (Spearman rank correlation 0.186) in the Gulf of Carpentaria, whereas the combination of water depth, percent gravel and seabed exposure was found to have stronger explanatory power (correlation 0.599).

3.2.5. Geophysical Properties and Sediment Fabric

The roughness of the sea floor is recognised as an important control on habitat type and biodiversity (Greene et al. 2007a). For soft-sediment substrates, seabed roughness can be caused by infaunal bioturbation at the local scale through to large bedforms such as sand waves (Table 3.4). Sedimentary bedforms such as ripples, dunes and sand waves are known to affect the abundance and distribution of benthic organisms by disturbing their habitat (Barros et al. 2004) or by influencing local circulation, larval dispersal and food supply (Vasslides & Able 2008). On Georges Bank, Thouzeau (1991) described a 10-fold decrease in megafauna density on sand dunes compared to more stable sandy bottoms. Kostylev (2001) recorded similar patterns between active bedforms and more stable areas for the Scotian Shelf. Combining parameters that describe bedform patterns and sediment grain size measurements represents a method of capturing information on both the physical and hydrodynamic characteristics of benthic habitats (Kostylev et al. 2001).

The sediment-organism relationships determining benthic assemblage distributions are often complex and involve geological, hydrodynamic, chemical and biological factors that may be difficult to measure. For many settings, sediment properties provide a useful first-order surrogate. The value of these parameters as surrogates can be significantly enhanced when they are employed in combination with other parameters, such as measures of the seabed hydrodynamic regime that better represent the complex ecological processes that control the distribution of benthic organisms.

Table 3.4. Examples of soft-sediment features of various scales that may have surrogacy value.

Feature	Linear scale (km)	Relief (m)	Sediment type	Formative process	Potential ecological impact	Example reference
Burrow mounds, holes & small bed irregularities	0.01-1	0.01-1	Mud, sand	Bioturbation; growth of sessile organisms	Local disruption of currents; alteration of surficial grain size; irrigation of sediments	Widdicombe *et al.* 2003
Sedimentary bedforms (ripples, dunes, sand waves)	0.1-1	0.1-10	Sand, gravel	Near bed current (wave, tidal or ocean current)	Unstable substrate	Thouzeau *et al.* 1991
Boulder and gravel beds	10-100	1-10	coarse gravel	Wave erosion; Sea level change	Local disruption of currents; potentially semi-consolidated	Green *et al.* 2007

3.3. Habitat Complexity

3.3.1. Geomorphology

Seabed geomorphology encompasses the shape and hardness of the seabed at a range of spatial scales and describes the processes behind these occurrences (Kennet 1982). At the broadest spatial scale, geomorphological features are categorical descriptors of the shape

of the seabed (e.g. reefs, ridges, seamounts) that describe structures that range in scale from thousands of km^2 (e.g. basins) to a few hundred m^2 (Harris et al. 2008). Seabed geomorphology can also be described by a range of parameters derived from various types of bathymetric, acoustic, video and seabed sample data. For example, seabed slope and roughness (rugosity) are parameters that can describe the structural complexity of the seabed over regional (100s of km) (Kukowski et al. 2008) to site-specific scales of a few metres (Holmes et al. 2008).

Rugose benthic habitats offer refuge from predators and settlement surfaces not available on flat bottoms. Seagrass beds, reefs, mangrove forests and algal assemblages are home to more species than the adjacent sandy or muddy substrate, accounting for increased richness at a local and regional scale. Seagrasses are poor as a source of food for grazing taxa (Fry 2006), but the vertical structure provided by plants offer habitat for edible epiphytes in addition to being a refuge from predation (Snelgrove 2001). Biogenic structures such as worm tubes, mussel beds and hard coral skeletons offer similar habitat advantages (Callaway 2006; Nakamura & Sano 2005; Reise 1981; Tsuchiya & Nishihira 1986).

Geomorphological parameters form useful surrogates where ecological processes are known or suspected to link seabed structure and the distribution of benthic communities. Seafloor topographic complexity is ecologically important because it provides habitat structure for juvenile and adult animals (Kostylev et al. 2003), plays a role in regulating foraging patterns (Erlandsson et al. 1999) and alters boundary-layer flow over the seabed (Green et al. 1998; Ke et al. 1994). The interaction of flow and substrate heterogeneity affects larval settlement and subsequent population performance because it controls delivery of food, oxygen, and chemical cues (Lenihan 1999). Seabed complexity also influences erosion, transport and deposition of sediment (Widdows et al. 1998) and macrofauna (Urbanski & Szymelfenig 2003). Importantly, as structural complexity shapes the perception and behaviour of benthic organisms it influences higher level processes of population dynamics and community structure (Kostylev et al. 2001). Areas of high species richness are often associated with habitat heterogeneity (Gladstone 2007) - the complexity of habitat can interrupt predator-prey relationships that in a simpler habitat might lead to clear dominance or removal of certain species. Thus, in complex habitats, species may co-exist in a greater diversity than they would in a simpler habitat (Peterson et al. 1998).

The spatial extent to which a geomorphological variable acts as a surrogate for a benthic assemblage or set of species is an important consideration, especially if there is no clearly defined process that explains the link between the physical parameter and distribution of biota (Holmes et al. 2008, Greene et al. 2007c). Links may not be direct, however, and geomorphic parameters may themselves be surrogates for other environmental factors directly controlling ecological processes: sand waves may be a surrogate for wave and current energy, and canyons structure may act as a surrogate for light penetration (Kostylev et al. 2001). Geomorphological surrogacy relationships can range in scale from biogeographic patterns that occur across ocean basins and seamounts (Etter & Mullineaux 2001) through to fine-scale patchiness in shelf benthic community types related to variations in habitat structure produced by the distribution of rocky and unconsolidated seabed (Ryan et al. 2007b). Most often, however, the performance of geomorphological parameters as surrogates is more effective when a combination of variables is considered or when they are considered in concert with sedimentological or oceanographic variables (Post et al. 2006, Greene et al. 2007c).

The delineation of seabed geomorphological features requires bathymetric data with a resolution that matches the scale of the features of interest. Typically, a seabed digital elevation model is derived from bathymetry data and classified using expert interpolation supported by various types of topographic feature algorithms (Lanier et al. 2007). For ocean-basin or global scale assessments of seabed geomorphology, broad-scale compilations of a wide range of data types have been used (Harris et al. 2008). For regional scale studies, a range of data types (hydrographic chart data, single-beam echosounder, multibeam) and resolutions are usually combined (Romsos et al. 2007). For sub-regional to local scales, multibeam sonar data are usually employed (Kostylev et al. 2001), while in shallow, clear-water settings, laser airborne depth sounder systems are often used (Walker et al. 2008). The advantage of multibeam and laser systems is that they can provide high resolution area coverage of accurate bathymetric data. Multibeam systems can also provide backscatter intensity data, which can indicate the texture and hardness of the seabed (Kloser et al. 2007). At regional to local scales, sidescan sonar images are very useful for identifying seabed textural patterns that are produced by both physical (sediment type, roughness) and biological features (macro algae, sessile fauna) (Prada et al. 2008). Local-scale geomorphic features may also be observed directly in towed underwater video footage (Anderson et al. 2007).

In terms of broad patterns in seabed biodiversity and geomorphology, recent studies of seamounts have shown several to be mid-ocean biological hotspots providing hard substrate for attaching organisms and creating a range of unique benthic environments in terms of energy regimes and rates of food supply through the interaction of the seamount topography and ocean currents (Clark et al. 2006). Similarly, structurally complex granite outcrops are characterised by benthic communities distinctly different to those living in the surrounding flat, unconsolidated seabed due to the formation of microhabitats by fractures and joints and enhanced food supply from the current flows around outcrops (Beaman et al. 2005).

Geomorphology often combines with other factors to be used as a successful surrogate. For example, the distribution of benthic communities in the southern Gulf of Carpentaria, Australia, was best explained by the influence on biota of different combinations of depth, bottom disturbance and seabed composition (Post et al. 2006). Similarly, in the northern Great Barrier Reef, seabed slope, in combination with the proportion of gravel and turbidity, is a major factor that influences the observed spatial distribution of megabenthos assemblages (Beaman & Harris 2007). In addition, Holmes (Holmes et al. 2008) used several geomorphological parameters to build predictive models of the distribution of a range of sessile communities in a marine park on the temperate inner and middle shelf of western Victoria, Australia. The best predictors of the main sessile communities in the park, as determined from towed video of the seabed, were found to be bathymetry (2 m grid), hypsometric integral (i.e., a non-dimensional measure of the proportion of an area that is above a certain elevation) (circular window radius 50m and 100m) and local relief (radius 100m) (Holmes et al. 2008). Similarly, quantitative morphological parameters (slope, rugosity, topographic position index) derived from multibeam sonar data collected on the temperate Oregon shelf discriminated a range of seabed structural features (ridge, boulders, cobbles) that form key refugia for several demersal fish species (Whitmire et al. 2007). Broad scale (1-10 km) benthic terrains on the deep-water areas of the continental slope of southeastern Australia, classified using 'soft', 'hard', 'smooth', and 'rough' parameters derived from multibeam sonar data, were shown to be good predictors of the distribution of benthic faunal groups

(Kloser et al. 2007). This approach represents an effective method of mapping seabed habitats and potential patterns of biodiversity in this vast continental slope environment (>150 m – 1000 m) at a scale useful for conservation management (Kloser et al. 2007). However, these parameters alone may not represent good predictors of the distribution of some faunal groups, and other substrate categories such as "mixed" may provide more useful information for use in management decisions (Greene et al. 2007a, b).

3.3.2. Spatial Heterogeneity

Spatial heterogeneity is often cited as a diversity driver, with high inshore species richness being promoted by the variety of habitats available on a broad scale and deep water benthic and planktonic richness occurring in spite of low biomass as a result of small scale shifts in sediment or water composition in habitats which otherwise appear homogenous (Snelgrove 2001). Rocky reef habitats are structured across a full spectrum of spatial scales, from sub-millimeter to the order of tens of meters, and these patterns influence the behaviour of benthic organisms, in turn influencing higher level processes of population dynamics and community structure (Knight & Morris 1996). Spatial pattern is difficult to quantify and refers to the spatial character and arrangement, position or orientation of patches within a landscape (Li & Reynolds 1993). Terrestrial landscape ecologists have long studied the effects of spatial pattern on process (With 1997) and have developed a large collection of metrics to describe landscape pattern (O'Neill et al. 1998). These metrics have proved useful for the description of landscape structure and its spatial dynamics over a broad range of spatial and temporal scales (Riitters et al. 1995). Landscape metrics applied to ecological studies fall into two general categories (Gustafson 1998): One quantifies the composition of a map with reference to spatial attributes, and the other category quantifies the spatial configuration of the map requiring spatial information for their calculation. There are many ways to define landscape depending on the phenomenon under consideration. The issue is that a seascape is not necessarily defined by its size but by an interacting mosaic of patches relevant to the habitat under consideration (at any scale) (Harris et al. 2008). Scale in remote sensing is typically defined by pixel resolution but objects have their own inherent scale, and the same type of objects can appear different at different scales (Lillesand & Kiefer 1994). For example, high frequency multibeam sonar data can be processed to < 1 m resolution implying that the minimum object that can be detected is twice the pixel size. In this case patterns in reef systems can likely be detected from individual reefs two meters and greater in size.

A greater understanding of the distribution and complexity of benthic habitats and a common approach to measuring and describing this complexity will provide a spatial framework within which to properly address spatially explicit research and management goals (Kendall et al. 2005). Conservation strategies now frequently consider not only amounts of habitat that must be retained but also the spatial configurations of habitats across depth and exposure gradients (Fortin et al. 2005). The decline of many species has been linked directly to habitat loss and fragmentation. Identifying what characteristics make an area preferentially habitable for particular species has been examined by many landscape ecologists and is being increasingly taken up by marine ecologists to describe patterns of benthic diversity (Barrett et al. 2001). Numerous indices of landscape pattern have been linked to ecological function by recent advances in image processing and GIS technologies. Studies indicate that abundance and species richness of reef fish are related

to habitat diversity (Ault & Johnson 1998), habitat extent (Tolimieri 1998), and habitat complexity (Jones & Syms 1998), but the value of such indices is yet to be incorporated into spatial analysis of marine ecological patterns. It may be true for the marine environment, as for terrestrial studies, that the distinction between what can be measured and patterns relevant to the ecological phenomenon under investigation is sometimes blurred (Levin 1992). Uncertainties in mapping the pattern and extent of marine habitats have, until recently, been behind the rarity of habitat-scale studies in marine ecology (Gray 2000).

3.3.3. Habitat Size

The species-area relationship represents one of the earliest quantitative models in biogeography, since a relationship between the number of species and land area was noted as early as 1778 (Brown & Gibson 1983). This was further developed into the equilibrium theory of island biogeography (MacArthur & Wilson 1963). This theory emphasises the importance of island area in combination with isolation, colonization rate and extinction rate as determinants of the equilibrium number of species. Extensions of this model treat species as functionally indistinguishable, only diverging through demographic stochasticity (Bell 2000). Thus, community composition is constantly changing over time as a dynamic balance between colonization and extinction (Kadmon & Allouche 2007).

Evidence for species-area relationships in the marine realm has been demonstrated for marine invertebrate communities associated with boulders (McGuinness 1984), rock walls (Smith & Witman 1999), mussel beds (Witman 1985), coral heads (Abele & Patton 1976) and for coral and reef fishes (Bellwood et al. 2005). Theories based on the species-area relationship have however been criticised for neglecting species-energy relationships (Kalmar & Currie 2006), small-island effect (Lomolino & Weiser 2001) and, above all, the fact that species differ functionally in how they interact with the environment in space and time (Gardner & Engelhardt 2008). The latter assumption forms the basis of the niche theory (Hutchinson 1957) which was recently coupled to the island biogeography theory into a unified general model (Kadmon & Allouche 2007). To successfully characterise a system based on abiotic variables, the area available to form particular habitats must be taken into consideration and the sampling scaled with this in mind (Thrush et al. 2005).

3.4. Disturbance

Dayton (1971) established space clearing disturbances as a key variable determining marine assembly structure. Storms and current eddies may contribute to primary space being made available in a system in two fashions: increasing sheer stress at the benthos/water interface, which can remove sediment, algal cover and motile fauna; and mechanical abrasion or damage caused by moving sediment or projectiles (Sousa 2001). Benthic space can also be made available in the wake of acute pollution events (Scanes et al. 1993), fishing activity (Currie & Parry 1996) and eutrophication (Tett et al. 2007), but the effects tend to be locally focused.

The intermediate disturbance hypothesis of Connell (1978) predicts maximum biodiversity at a frequency of disturbance where recruitment is able to replace lost individuals but inter-specific processes don't have time to exclude species. This response has been recorded in many marine systems (Begon et al. 1996; Gutt & Piepenburg 2003;

Svensson et al. 2007). Disturbance, both anthropogenic and natural, may act as a potential abiotic surrogate for diversity at an appropriate spatial scale and temporal scale (Harris et al. 2008). For example, bed shear stress was found to be of use as an explanatory variable in fish occurrence prediction on the Great Barrier Reef (Pitcher et al. 2007). National indices of disturbance and exposure are currently being developed through Geoscience Australia's GEological and Oceanographic Model of Australia's Continental Shelf (GEOMACS), with general predictions that biodiversity will be highest in areas of intermediate disturbance (Connell 1978).

The stability of the seabed sediment surface exerts a major control on benthic community structure (Newell et al. 1998). Species diversity tends to be highest on stable rocky shores and on cohesive muddy shores, with the more mobile sandy or fine gravel substrates typically showing much lower richness. Sediment stability is dependent on slope, particle size and the degree of water motion on the bed (Bagnold 1963). The shape and roundness of sediment grains are additional properties that determine the stability of a deposit (Lewis & McConchie 1994) but grain shape is difficult to measure and is rarely recorded despite its likely importance. Stability may also be influenced by the presence of biota through biological armouring of the bed and binding of sediment by faunal mucus (Murray et al. 2002). The stability of a sediment surface as a habitat is difficult to quantify, particularly given that one of the key proxies, sediment grain size, is determined on disaggregated samples which have been dislodged from their environment and may have little physical resemblance to what an organism actually encounters (Snelgrove & Butman 1994). Laboratory experiments of near-bed flow and sediment stability in relation to settlement of benthic organisms (St-Onge & Miron 2007), and field verification of the results is required to test their utility as surrogates (Post et al. 2006).

3.5. Productivity

3.5.1. Primary Productivity

Opposite to patterns observed for terrestrial systems (Currie et al. 2004), high primary productivity in near shore waters tends to promote low species richness (Snelgrove 2001) and high evenness (Hillebrand et al. 2007). In these areas the role of producer tends to be dominated by a small number of species able to monopolise resources under ambient conditions. Corresponding benthic communities are dominated by the taxa best able to use the associated products (Lenihan & Micheli 2001) or withstand periods of anoxia imposed by excess organic input (Dell'Anno et al. 2002). In contrast, oligotrophic waters are often home to low biomass assemblages with high species richness, including a large proportion of endemic taxa (Poore et al. 2008). Coral reefs, areas of high biomass and species richness occurring in oligotrophic waters, are an exception. The symbiosis between coral polyps and their resident zooxanthellae allows higher productivity than would otherwise occur in the ambient conditions and the spatial complexity and diversity of habitats provided by hard corals competing for space and light promotes a high corresponding richness of invertebrate and fish life, in turn supporting a rich community of predators (Cribb et al. 1994). Primary production can be estimated from satellite or airborne spectral analysis of chlorophyll in surface waters (Parmar et al. 2006). While productivity is directly linked to marine biodiversity, the relationship has yet to be fully explored as a predictive surrogate over large scales.

3.5.2. Organic Carbon

Detrital matter derived from primary productivity and the wastes of secondary production comprise a valuable resource in the photic zone and, excepting chemosynthetic systems, almost the only energy input to the aphotic zone (Carney 2005; Vetter 1995). This material settles in particles of various sizes, among which larger particles such as faecal pellets (Angel 1984) and marine snow (Alldrege and Silver 1988) are particularly important. It is generally accepted that the flux of particulate organic carbon (POC) from the euphotic zone controls the biomass and abundance of deep-sea benthos. This notion was originally based on observations of high benthic standing-crops beneath productive equatorial and near-shore waters, and low standing-crops underlying oligotrophic gyres (Belyayev et al. 1973; Hessler 1974; Gage and Tyler 1991; Rowe et al. 1991; Blake and Hilbig 1994). However, a direct coupling between pulse-like sedimentation events and the activity of benthic fauna has become clear in recent years (Aberle and Witte, 2003 and references therein). The detailed nature of this coupling remains poorly understood because there have been few studies which combine both types of measurements. One good example is a study by Smith et al. (1997) in the equatorial Pacific, in which strong and significant correlations (r^2>0.9) were found between both megafaunal- (phototransects) and macrofaunal (enumerated from box core samples) abundances and annual POC fluxes. An interesting conclusion from this study was that macrofaunal abundance might potentially serve as a proxy (i.e. surrogate) for POC flux in low energy abyssal habitats, implying that the macrofauna themselves are either more widely or more easily measured than POC fluxes (see also Rowe et al. 1991; Cosson et al. 1997).

The main way to directly measure POC fluxes is using sediment traps, and at the time of the Smith et al. (1997) study, approximately 37 records integrating annual time scales existed in the open ocean (Lampitt and Anita 1997). More recently, Seiter et al (2005) drew on particle-trap data from 61 locations, and produced a global map of minimum POC flux to the seafloor which was based on global estimates of diffusive oxygen uptake. This map, and the global map of total organic carbon (TOC) concentrations that underpins it (Seiter et al. 2004), may prove useful in making first order approximations of benthic productivity over broad scales, assuming that benthic communities are not compromised by sediment de-oxygenation. Indeed, the relationships between diversity and POC fluxes (or other productivity proxies) are scale-dependent and may be complicated by other variables that influence diversity including bottom-water oxygen concentration, hydrodynamic regime and the stability of the physical environment (Levin et al. 2001). The study by Smith et al. (1997) of the abyssal equatorial Pacific was unique in the respect that the productivity gradient found there varied independently of other influential factors. Thus, the uni-modal relationships between productivity and diversity expected over broad scales in the deep sea are plausible but are not well substantiated due to: (i) the complexity of interacting factors; and (ii and iii) an inability to both clearly identify mechanisms through which productivity influences deep-sea diversity, and to accurately place available studies in a continuous productivity gradient (Levin et al. 2001).

Proxies of POC fluxes such as TOC, TOC:TN ratios, biochemical markers and pigments in sediment have proven useful in explaining more localized patterns of biodiversity. TOC is undoubtedly the most widely measured of these parameters (Seiter et al. 2005), and, where a consistent and robust method (Galy et al. 2007) has been applied to its measurement, TOC can be a useful surrogate for biomass, deposit-feeding taxa, and

community structure (Gogina et al. 2010). However, its application is limited to interpolations from physical samples (Levin and Gage 1998) as no remote sensing proxy is available. Moreover, correlations between TOC and diversity measures are not always found (Cartes et al. 2002; Danovaro et al. 1995) because a large proportion of TOC in sediment may be refractory and thus resistant to bacterial degradation. Sediment grain size can also affect the amount of biologically available organic matter (OM) in shallow soft sediments (Taghon 1982). Small particles have larger surface area per unit volume than large particles, offering greater habitat for micro-organisms (Fauchald and Jumars 1979; Neira and Hoepner 1994; Petch 1986) and associated organic matter. Some deposit-feeding species use size-specific foraging mechanisms to select and ingest fine sediments (Butman and Grassle 1992; Sebesvari et al. 2006; Thiyagarajan et al. 2005), but both selective and non selective deposit feeders exhibit settlement preferences for sediments with high concentrations of readily available organic carbon (Post et al. 2006; Snelgrove and Butman 1994).

The availability, freshness or quality of OM pertains to the labile fraction, which consists mainly of lipids, carbohydrates, proteins and nucleic acids (Danavaro et al. 1993; 1995; 2001). Several useful biochemical parameters have been derived to describe the lability of OM (Cowie and Hedges 1992; Danavaro et al. 1995; Wakeham et al. 1997; Dauwe et al. 1999), and some of these have proven useful for explaining different diversity indices (Danovaro et al. 1995; Cartes et al. 2002). Such measures, however, often require a high degree of discipline expertise (and advanced techniques), and as such are unlikely to be widely employed in the capacity of surrogates. However, the Chlorin Index (CI) (Schubert et al. 2005) is a simple analytic measurement of OM lability, whose reliability has been demonstrated by comparison to more advanced techniques (e.g. Dauwe Index, total hydrolysable amino acids, and % ß-alanine as non-protein amino-acid, and sulfate reduction rates) (Schubert et al. 2005). It is a measure of the amount of chlorophyll (and its degradation products) that could be transformed to phaeophytin, and is expressed as the ratio of the fluorescence intensity of a sediment sample extracted in acetone and subject to HCl treatment to that of the original sediment sample (Schubert et al. 2005). CIs were found to correlate well with an index of track richness developed from photographic stills of seabed sediments, which conveyed differences in the diversity of tracks, faecal casts, burrows and mounds of benthic biota in deep-sea sediments of the Lord Howe Rise (Dundas and Przeslawski 2009). Comparison with this index shows a greater diversity of animal traces, and potentially more metazoan activity, in sediments of apparently higher food quality. CIs thus show promise as an easily measured geochemical surrogate of biodiversity for regions where organic loads are not expected to give rise to significant sediment anoxia.

3.6. Oceanography

Oceanographers measure and model variables that directly influence the physiology and behaviour of marine organisms (temperature, salinity, pH), variables affecting productivity (nutrient concentrations, temperature and light intensity: see section on productivity) and the currents that affect larval distributions. Some factors (pH and salinity) vary sufficiently over regional and global scales to show correspondence to biological patterns (Williams & Bax 2001) but are sufficiently uniform at a local scale (with the exception of estuarine systems) to preclude their use in local surrogacy analyses

(Bamber et al. 2008). Dissolved oxygen has been identified as a key predictor of biodiversity in deep sea sediments (Levin & Gage 1998).

In addition to determining local water properties and delivering food and oxygen, ocean currents are important to the dispersal of many marine organisms which, in turn, determines the potential distribution of many benthic taxa. Most larvae and algal propagules spend their early development adrift and must attempt to settle where the prevailing currents take them. With larval periods ranging from hours (e.g., tropical ascidians in Cloney et al. 2006) to four and a half years (e.g., gastropod in Strathmann & Strathmann 2007), the scope for currents to act as a surrogate for potential richness is substantial where both life histories and water movements are well known. The relative rarity of long larval life histories make local currents (~tens of kilometers) more important than regional currents in determining benthic larval supply (Palumbi 2001), but even groups with well known life histories have frustrated attempts to predict geographic assemblies (Shulman & Bermingham 1995). Stevens and Connolly (2004) considered local scale current speed as an abiotic variable in their assessment of surrogates in Moreton Bay, Australia, but found its predictive capacity negligible. In addition to understanding larval supply patterns, the proximity of any given sample to diversity hotspots must be taken into consideration (Bellwood et al. 2005).

Further information on biodiversity patterns as they relate to oceanographic variables can be found in reviews by Hall (1994), Wolanski (2001), and Levin et al. (2001).

4. Utility Considerations

4.1. Temporal Variations

Knowledge of temporal variation in potential surrogacy relationships is limited. Most of our knowledge of the temporal variations in marine biodiversity comes from intertidal habitats, where some assemblages show pronounced seasonal changes, e.g. nematodes (Hourston et al. 2005), and some other systems show no seasonal variation, e.g. flatworms (Dittmann 1998). Although, we have a good understanding of temporal variation in broad processes such as organic input (Gooday 2002) and numerous studies investigate the relationships between abiotic and biotic factors (see previous sections in this review); we still have limited understanding of how such relationships change over weeks, seasons, and years.

Consideration of temporal variation increases our chances of identifying surrogacy relationships. Some relationships may change or only be detectable during certain times of day, seasons or years, likely due to phenology of biota or inter-annual variations in climate, recruitment, and other processes. Diurnal patterns may play an important role in the detection of surrogacy relationship, particularly regarding sampling mobile organisms. The composition of deep sea demersal fish changes between night and day (Suetsugu & Ohta 2005), and the interpretation of data will therefore depend on the diurnal variation of an assemblage and the timing of sampling.

Seasonal patterns also play an important role in the abundance of many taxa, particularly in shelf waters where benthic communities can be highly regulated by seasonal upwelling and thermal changes. Reproduction of some deep-sea animals are apparently synchronised with the seasonal sinking of phytoplankton blooms at the surface (Turner 2002). Seasonal variation in potential surrogacy relationships may also be related to depth. In the eastern Mediterranean, both abiotic factors and detritus-driven relationships in mesozooplankton vary among seasons in the upper 750 m (Koppelmann & Weikert 2007). Between 750-1050 m, differences between seasons were not detected, while deeper waters between 1050-2250 m showed a slightly later seasonal increase in abundance than upper waters, likely due to lag between bloom events and the arrival of their products. No temporal changes in abundance were detected below 2250 m (Koppelmann & Weikert 2007). Seasonal variations in abundance and community composition at the bottom may mirror variations noted in zooplankton communities across various depths, but further research is needed to test this hypothesis.

On a larger temporal scale, inter-annual variation has been detected in many communities, including homogenous muddy sand, in which large infauna were neither spatially nor temporally uniform (Parry et al. 2003). The causes underlying such temporal variation remain unknown but may nevertheless affect the detection and utility of surrogacy relationships.

The magnitude of temporal variation may be related to organism size. On the abyssal plain, the abundance of meiofauna and near-surface deposit feeders spiked during the annual pulse of organic input, while the abundance of macrofaunal polychaetes increased much more gradually, lagging behind the pulse (Galeron et al. 2001). In a review of soft-sediment community responses to organic input, Gooday (2002) showed that temporal patterns between biotic and abiotic factors vary according to size classes, specifically that only bacteria and foraminifera show a consistent and direct response to seasonal organic inputs, while populations of larger fauna generally show reduced,

lagged, or unmeasurable responses (Gooday 2002). In contrast, Grove et al. (2006) found the abundance of microbes and meiofauna is not correlated with organic content in Chatham Rise, eastern New Zealand, suggesting that size-dependent temporal patterns in abundance may vary across regions, depths, and habitats. Assuming niches will be filled by functionally equivalent or related organisms through time and assessing biota in terms of functional groups or at coarse taxonomic resolutions may offer a means to circumvent this shortfall.

4.2. Surrogacy in the Deep Sea

The relationships between abiotic and biotic variables can be quite different in deep and shallow waters. Compared to shallow water fauna, deep water fauna live in darkness at relatively stable temperatures in the absence of phytoplankton and other photosynthetic organisms. Thus, potential surrogates for shallow water biodiversity, such as temperature, wave action, depth (as a proxy for light attenuation), and primary productivity may not apply to deep sea biodiversity. Conversely, factors such as organic composition of sediment may have far more importance in deep-sea environments, in which deposit-feeding species dominate (Levin et al. 2001).

Potential surrogate relationships are far less well-known in deep waters (>1000 m) than in shallow waters, probably due to the comparative difficulty of sampling biota and the lack of knowledge of taxa and life histories. The few studies that do investigate surrogacy in the deep-sea have focused primarily on depth (Brandt et al. 2007), and most are from the northern Atlantic (Levin et al. 2001) or Antarctic regions (Ellingsen et al. 2007) particularly at chemosynthetic or ephemeral habitats such as hydrothermal vents, cold seeps, and whale falls. Increasing efforts are being made to characterise deep water biodiversity as nations seek to manage the resources of their exclusive economic zone.

4.3. Surrogacy across Spatial Scales

Quantification of spatial scale depends on three characteristics: 1) the size of each sample, 2) the distance between samples, and 3) the total area encompassing all samples (Parry et al. 2003). The importance of spatial and temporal variability has been recognised in terrestrial surrogacy research (Ernoult et al. 2006), with broad spatial scales associated with better performance of abiotic surrogates (Sarkar et al. 2005) and increased effectiveness of lower taxonomic resolution (Larsen & Rahbek 2005). Unfortunately, very little is known about differential surrogacy relationships across broad and fine spatial scales in the marine environment. Freshwater studies suggest that broad spatial scales are more useful to detect community patterns than local scales (Paavola et al. 2006), but it is unknown if this applies to marine systems. The influence of energy availability has been shown to differentially affect faunal distributions across spatial scales in the Mediterranean (Gambi & Danovaro 2006), suggesting that the detection of relationships between abiotic and biotic factors is dependent on the spatial scale used. Marine invertebrates show differential variability across spatial scales according to phylum (Anderson et al. 2005), and this variability is likely to be regionally-specific. For example, tropical Australian sponges are best represented at a medium scale of diversity, rather than at local or coarse regional scales (Hooper et al. 2002). The ability to use surrogates effectively at fine spatial scales may be related to the heterogeneity of a given area. Nevertheless, research in the northeast Atlantic found a high level of community

patchiness in a very homogenous soft sediment environment, highlighting the need to consider physical processes that operate on broad spatial scales as well as biological processes that operate on finer scales (Parry et al. 2003). There has been no concentrated effort to understand how spatial scale affects surrogacy relationships in the marine environment.

The effects of spatial scale on surrogacy relationships obviously have important ramifications for the detection of any such relationships (Gambi & Danovaro 2006). Many benthic species are restricted to a very small proportion of sites sampled (e.g. polychaetes and isopods in (Ellingsen et al. 2007), isopods in (Brandt & Schnack 1999), and it would not be practical to use such species to investigate surrogacy relationships except at extremely fine scales. In addition, consideration of spatial scale is crucial not only to evaluate the utility of a potential surrogate, but also to appropriately address the research hypothesis or management strategy. For example, if surrogacy research is needed to better inform the design of protected areas within a bay, basin, or other relatively small area, a regional spatial scale may be too large (Greene et al. 1999).

4.4. Combined Effects of Potential Surrogates on Benthic Biodiversity

Some physical factors may interact to synergistically or antagonistically affect fitness, fecundity, behaviour, or demography of one or more species (Folt et al. 1999); but until recently most surrogacy research has focused on only one variable at a time. In many aquatic communities, biodiversity and biogeography are best associated with multiple environmental factors and rarely defined according to just one (Dauer et al. 2000; Hagberg et al. 2003; Kennard et al. 2006).

Abundance of certain species may correlate with abiotic variables such as depth and organic carbon flux, but the actual cause of these relationships may be due to a biotic factor such as predator density which is itself directly regulated by abiotic factors (Micheli et al. 2002). Many sessile invertebrates provide habitat and food to other fauna so the presence of these habitat-forming invertebrates directly affects the abundance of other invertebrates and fish (Tissot et al. 2006, but see Jensen & Frederickson 1992; Klitgaard 1995). The presence of infaunal species can change the sediment composition and ecology, thus making it difficult to determine causes and effects (Bremner et al. 2006). In addition, biological processes in separate oceanic zones can affect each other. Benthic-pelagic coupling is well-studied across a variety of systems (Turner 2002), and the contributions of pelagic detritus to benthic processes are extremely variable and affected by several interacting factors, including pelagic community composition, trophic interactions, sinking rates, and oceanographic conditions (Turner 2002). Indeed, the bathymetric zoning of deep-sea fauna has been linked to increasing pressure and decreasing food availability with depth (Carney 2005). Identification of potential surrogacy relationships is only the first step and is relatively straightforward compared to the interpretation of such relationships, due to the linkages between some abiotic factors and physical and biological processes (Figure 1) (Hagberg et al. 2003; Levin et al. 2001). Nonetheless, understanding the causes underlying surrogacy relationships, including interactions between multiple abiotic and biotic variables, will enhance our ability to develop predictive models across a range of systems (Parry et al. 2003).

4.5. Utility of Different Sampling Regimes

Biological sampling can be undertaken through both destructive and non-destructive methods at a broad range of spatial scales. The nature and strength of surrogacy relationships may vary across sampling regimes because each sampling method is associated with discrete optimal habitats and taxa. For example, most grabs target sessile epifauna and small infauna and tend to underestimate larger sedentary animals due their ability to bury deeper than the sampler penetrates (Parry et al. 2003). Tracks, mounds, and burrows can be used to gauge benthic activity (Parry et al. 2003), but the persistence of biological structures is related to currents and disturbance, as tracks will persist far longer in low disturbance environments (e.g. deep sea habitats) (Dundas & Przeslawski 2009, Wheatcroft et al. 1989). Thus, the correlation between tracks and biodiversity will be more immediate in high disturbance environments and detection of associated surrogacy relationships may vary with disturbance rates across regions. To date there has been little research investigating whether sampling methods vary in their suitability to detect relationships between physical surrogates and biodiversity of marine benthic communities. Such research will provide valuable insight into the appropriate methods to use for biological collection, as well as proper interpretation of data analyses and perhaps lead to distinct biodiversity concepts being mated to particular samplers.

Regardless of the sampling method used, species accumulation curves are important to compare diversity among habitats, particularly among large bathymetric gradients. Species accumulation curves display the number of species encountered with increasing sampling effort; an area is considered well-sampled when the curve asymptotes. They are important tools to identify the effectiveness of biodiversity estimates. For example, in a comparison of shallow- and deep-water diversity, even when sampling was conducted for the same duration, diversity may still not be comparable if the species accumulation curve for the deep-water system has not yet reached its asymptote (Levin et al. 2001).

The application of technologies that increase the data returned per unit effort of sampling: e.g. multibeam sonar (Kostylev et al. 2001), acoustic Doppler current profilers (Harris et al. 2008) and airborne remote sensing (Mumby et al. 1997); allow potential surrogates to be nominated and tested. Biological data remains the limiting factor, but targeted surrogacy research is gradually revealing species richness patterns that contribute to our understanding of ecological processes and the identification of effective prediction tools with which marine biodiversity can be managed in an informed fashion.

4.6. Management Decisions at Various Scales

The merit of researching surrogacy relationships is the increased capacity to manage marine resources with confidence that biodiversity concerns have been adequately addressed. This confidence will vary according to how well the information required to meet goals of marine resource managers has been addressed by surrogacy research and by the scale at which a decision is expected to influence environmental outcomes. While biogeographic maps and classifications have been widely applied to natural resource management in terrestrial systems (Vierros et al. 2008), their application to marine resources is still developing. Here, the use of surrogate variables in marine resource management is examined using examples at increasing spatial scales.

Until 2002 most coastal waters of Victoria (Australia) were legally regarded as unreserved public land (Environmental Conservation Council 2000). The Victorian Environment Conservation Council adopted a community, habitat and ecosystem approach to categorising Victorian marine resources and choosing sites for marine protected areas along the Victorian coast (O'Hara 2000). This strategy was chosen because habitat protection was thought to be a sound means of maintaining existing biodiversity (Environmental Conservation Council 2000), defined as "the natural diversity of all life: the sum of all our native flora and fauna, the genetic variation within them, their habitats, and the ecosystems of which they are an integral part," and because of the difficulty involved in describing the highly endemic local marine flora and fauna at the species level (Poore & O'Hara 2007). Extensive species level surveys and genetic studies were acknowledged as a possible route to defining aspects of biodiversity missed by habitat level characterisation but these could not be applied as widely or quickly as required. An existing model of five coastal bioregions defined by bathymetry and benthic macrofauna distributions was therefore used to establish thirteen Marine National Parks and eleven Marine Sanctuaries protecting 5.3 % of the Victorian coast (Ferns et al. 2003) under the *National Parks Act 1975* (Vic).

Focusing on a broad scale definition of biodiversity allowed the Environment Conservation Council to create a management strategy in a timely fashion at the expense of the ability to manage resources at the species level, although the protected area selection criteria applied to Victoria's marine resources had sufficient flexibility to allow management decisions to take into account individual species with an eye for large, charismatic taxa such as the giant kelp and the weedy seadragon (Ferns et al. 2003).

Terrestrial resource regionalisations have led the way in surrogate-based management of biodiversity at regional scales. It has tended to use some biological attributes along with physical attributes within a classification to produce regions (Ferns 1999). While the vast majority of national level work has been land-based over the past 50 years, marine classification maps of some form have been produced for most of the world's shelf waters (Vierros et al. 2008). Regionalisations have been made using numerical classification techniques or through the synthesis of patterns and processes by experts. Utilizing existing knowledge and classifications, and bringing together experts from each jurisdiction to assimilate and combine existing classifications into single national regionalisations has been the most successful approach for achieving useful outcomes. The Interim Biogeographic Regionalisation for Australia (Thackway & Cresswell 1995) and the Interim Marine and Coastal Regionalisation for Australia (IMCRA 2006) provided sufficient scientific synthesis of known biophysical attributes while also acknowledging and utilizing existing classifications at the State level. Both projects were developed to assist in planning national systems of protected areas, terrestrial and marine respectively, in accordance with several national and international environmental obligations (Creswell & Thackway 1998). Both of these regionalisations have been updated in recent years and extended through the addition of new information and levels of detail (Heap et al. 2005).

Perhaps the best measure of the usefulness of any classification or regionalisation is not in the exact nature of the boundaries that have been created either by computer or human eye, but rather in their application in biodiversity management. These regionalisations have been adopted and used for a multitude of conservation and sustainable use purposes at national and regional levels, and are now widely accepted as the standard biogeographic framework for use in both scientific and management studies.

In international waters biological sampling has been disparate (Harris et al. 2007b) other than around novel features, such as seamounts (Rowden et al. 2005) or hydrothermal vents (Van Dover 2000). Surrogate-based management of biodiversity is the only practical means to make reasoned decisions about high seas resource management. To fulfil their obligations under the United Nations Convention on the Law of the Sea, nations that use high seas resources are expected to monitor that use and put in place mechanisms to protect marine resources beyond their national boundaries (Ardron et al. 2008), but the biological information required to establish effective networks of protected areas does not yet exist (Harris et al. 2007a). Global regionalisations of high seas resources have a long history but have only recently applied spatial approaches to their classifications (Table 4.1).

Table 4.1. Approaches to classifying regions in the high seas (after Vierros et al. (2008)).

Project	Basis of zonation	Reference
Zoogeography of the Sea	Intuitive divisions of faunal zones	(Ekman 1953)
Marine Biogeography	Review of the work of Eckman and others	(Hedgpeth 1957)
Marine Zoogeography	Taxonomic biogeography	(Briggs 1974)
Classification of Coastal and Marine Environments	Spatial approach to Brigg's work	(Hayden et al. 1984)
Large Marine Ecosystems	Bathymetry, hydrography, productivity, trophic dependence	(Sherman & Alexander 1989)
Global Representative System of Marine Protected Areas	Intuitive consideration of biogeographic representations	(Kelleher et al. 1995)
Ecological Geography of the Sea	Surface productivity	(Longhurst 1998)
Ecoregions: the Ecosystem Geography of the Oceans and Continents	Latitudinal belts and patterns of oceanic circulation	(Bailey 1998)
Marine Ecosystems of the World	Review of previous work and intuitive input from experts	(Spalding 2007)
High Seas Marine Protected Areas	Multivariate analysis of depth, slope, sediment thickness, primary productivity, seabed temperature and dissolved oxygen	(Harris & Whiteway 2009)

The 53 713 polygons resulting from Harris & Whiteway (2009) were used to identify hotspots of habitat heterogeneity, potential candidate areas for international protection. Spatial classifications have been used to establish marine protected areas in the high seas (Ardron et al. 2008), but considerable effort and money will be required to police resource use and make high seas marine protected areas more than paper parks (Mossop 2004).

Various different numerical classification techniques have been used in an attempt to reach the holy grail of geographic regionalisation that can explain the distribution of the biotic realm in space and, for the adventurous, time. No single classification methodology has gained universal acclaim. The classification of a set of thematic environmental attributes recorded at a multitude of sites or taken from a uniform grid has been undertaken at a variety of scales as the basis for nature conservation planning and management (Lewis et al. 1991; Lyne & Hayes 2005; Mackey et al. 1988; Mackey et al. 1989; Thackway & Cresswell 1992). To date no numerically produced regionalisation or assessment has been widely adopted for use in biodiversity management. The reasons for this are complex and relate to the significant difficulties in utilising the correct combination of attributes in a classification that will replicate the patterns and processes recognized by humans, as well as institutional and governance complexity in how we manage biodiversity.

5. Synthesis

When decisions about the conservation or use of an area must be made, information about the biodiversity values of that area may not exist or be ignored, thereby hindering the development of appropriate resource management plans. This is often the case in marine benthic systems as they are difficult and therefore expensive to study and often have poor historical coverage compared to their terrestrial or pelagic equivalents. Exploring new ways of measuring and understanding the relationship between biota and the physical environment offers an opportunity to address challenges for biodiversity management using existing and easily gathered data. Surrogacy research is a rapidly-growing field, and useful relationships have been identified in several habitats, particularly with regard to sediment parameters. Some variables with direct influence on presence and abundance of benthic species (temperature, salinity, pH) vary over spatial and temporal scales that make them appropriate to apply at regional scales. Their broader influence can be invoked from less directly influential variables that correlate to longer or larger trends (depth, latitude, oceanic currents), but at those scales, confounding factors (larval/propagule supply, proximity to diversity hotspots) must be taken into account.

The use of remote sensing of chlorophyll-*a* as a surrogate of benthic biodiversity is hampered by poor understanding of the relationship between primary productivity and benthic assemblies. The general model of higher benthic richness in areas of lower productivity, an inversion of that observed in terrestrial systems, is too readily confounded by other variables to be confidently applied to management decisions.

The relationship between acoustic data and variables with direct (sediment hardness, rugosity and slope) and indirect (depth) influence on benthic assemblages, coupled with recent advances in our ability to map large areas of the seafloor using acoustic equipment offer the greatest potential for surrogacy based management of marine biodiversity. Ground-truthing of habitat classifications being derived from acoustic

mapping is an important but painstaking process, hampered by gaps in our knowledge including the difficulty of identifying organisms to fine taxonomic levels and the comparative shortage of information about meiofauna, microorganisms and deep sea ecosystems.

Patterns of benthic biodiversity observed in many regions today may not reflect the distribution and diversity of species of just a few decades ago, as overfishing, trawling, introduced species, and climate change have altered habitats. Therefore, physical surrogates of present-day patterns of biodiversity may carry some uncertainty about the degree of impact study areas may have suffered. Impacts affecting areas studied to refine abiotic surrogacy models must be considered before predictions based on those relationships are scaled beyond the impacted areas. Predictions of patterns of biodiversity based on surrogacy relationships may be considered 'potential' patterns that may occur in impacted areas when environmental pressures are reduced.

The range of biodiversity concepts and metrics available make choosing an appropriate approach to gathering and interpreting surrogacy data challenging. The results of any management decision should be kept in mind – is the system in question being managed to protect a particular habitat, for maintenance of ecosystem services, to create refugia for genetic diversity, or to insure particular taxa against extinction? – when a biodiversity measure is being considered. A thorough knowledge of the mathematical properties of that measure should inform any subsequent analyses based on it.

Our ability to measure abiotic variables in marine systems and our understanding of the relationships between those variables and biodiversity have increased with our need to make predictions about biodiversity in otherwise unsampled areas. The first test of abiotic surrogacy involves validating those predictions. The second test will be whether or not predictions based on abiotic surrogates are found to be useful in marine resource management.

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