



Census of Antarctic Marine Life (CAML)

Methods for defining marine benthic habitats: A review of current literature

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This document was prepared for another purpose, however it contains information of relevance to habitat mapping in the CAML project.

Introduction

Defining the interrelations between marine benthic organisms and the sea floor environment has important applications for the management and conservation of marine habitats. Our knowledge of the distribution, abundance and diversity of marine organisms remains sparse, primarily because it is time consuming and expensive to collect and identify the huge range of biological specimens which may inhabit an area. The relationship between benthic biota and the sea floor environment provides the possibility that the distributions of the biota may be predictable, given the measurement of the relevant physical parameters. Certain physical parameters can be measured much more easily than biological data and across wider areas, so use of these physical surrogates for community composition may provide a more complete coverage of marine ecosystems, allowing a more rigorous approach to the selection of Marine Protected Areas (MPA's).

However, the relationship between benthic fauna and physical properties is not well established, with many different environmental associations determined for different regions and organisms (eg. Webb et al., 1976; Grebmeier et al., 1988; Thouzeau et al., 1991; Snelgrove and Butman, 1994; Ambrose and Renaud, 1995; Long et al., 1995; Kostylev et al., 2001; Williams and Bax, 2001; Hill et al., 2002; Pitcher et al., 2002; Ramey and Snelgrove, 2003). For successful ocean's management a systematic approach is required to better define the links between abiotic and biotic factors. In this review, I firstly outline the methodologies for collecting and analysing physical and biological information and their application in marine management, I then discuss some of the key associations between biota and their physical environment, and finally I describe key indicators of disturbance and their impact on benthic communities, as this is an important part of managing and assessing risks to marine ecosystems.

In discussing the relationship between the biota and their physical habitats I draw largely on data and studies from the Gulf of Carpentaria, Australia. This area is one of the most broadly sampled areas on the Australian margin for benthic biota and

physical parameters, so provides a good basis for establishing physical surrogates for biological distributions and diversity. The area is also part of the Northern Planning Area, which is a current focus for regional marine planning by the National Oceans Office, with the final Northern Regional Marine Plan due to be released by the end of 2005 or early 2006. There are also several competing values in the Gulf of Carpentaria, with a multi-million dollar prawn industry, the most valuable prawn industry managed by the Australian Government (McLoughlin, 2004), onshore mining for bauxite, zinc, lead, silver, aluminium and manganese with associated shipping (National Oceans Office, 2003), and unique ecosystems including submerged reefs which support diverse coral communities (Harris et al., 2004), large populations of dugongs (Saalfeld, 2000) and nesting and foraging sites for marine turtles (Limpus and Chatto, 2004). Understanding the diversity and sensitivity of habitats in the Gulf is important for the sustainable management of this region, and the lessons learned can be well applied to other regions.

Reconnaissance mapping

One of the fundamental controls on seabed communities is the nature of the seafloor substrate. In general terms, the life habitat modes of organisms (sessile or attaching) limits their distribution to soft versus hard substrates respectively, since the attaching forms need something solid to cling on to, while the sessile forms tend to burrow in the sediment and forage within it for food. These associations are not exclusive, since attaching forms may attached to scattered cobbles or larger shells, however, the abundance of attaching faunas tends to be much greater on harder substrates. Habitats can therefore be differentiated at a broad level based on a knowledge of the substrate properties. Several mapping techniques are useful for this reconnaissance scale mapping of the seabed structure, and provide the basis for more detailed sampling.

Sidescan

Sidescan sonar images are commonly used to image seabed structures, sediment composition and biological cover (eg. Greene et al., 1995; Nitsche et al., 2004; Penrose et al., in press). The sea floor morphology is imaged particularly well by sidescan sonar, particularly for objects with significant vertical relief such as reefs (Penrose et al., in press). Other outcrops, such as bedrock, can also be distinguished, in addition to features such as landslide scarps, debris, faults and folds which are identified based on the strength of the backscatter and shadows on the profiles (Greene et al., 1995). Images from sidescan sonar have also been interpreted successfully to determine the boundaries of densely populated sea grass meadows and the height of canopies based on shadow length (Penrose et al., in press). However, it can be difficult to interpret the extent of biological communities where cover is sparse.

The interpretation of sediment types based on acoustic backscatter signals can also be difficult. Returns from sand waves and ripples, for instance, are similar to those from reef structures covered by a thin sand layer or reefs near the seabed (Penrose et al., in press). In a study in the Hudson River estuary, Nitsche et al. (2004) found that grain size did not always relate to differences in sidescan backscatter. Through the integration of sidescan backscatter, bathymetry and sub-bottom profiler data, however, they were able to better characterise the sedimentary processes (Figure 5). The sidescan backscatter correlated well with depositional and erosional processes as identified from sub-bottom profile data. The soft, water-rich nature of recently

deposited sediments caused low backscatter amplitudes, while high reflectivity occurred on eroded surfaces which comprised more compacted, harder sediments.

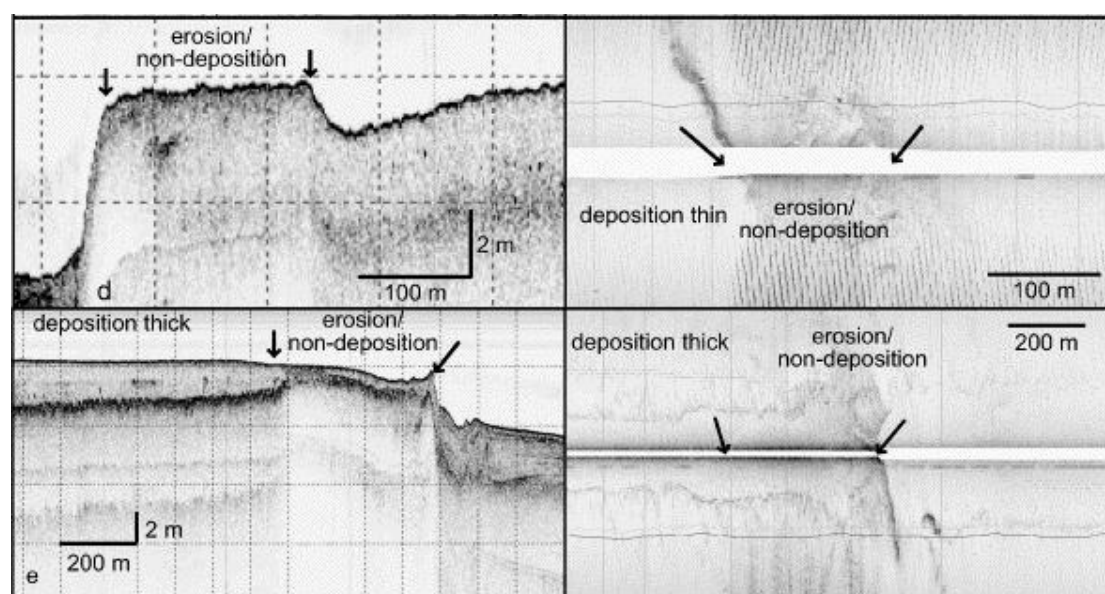


Figure 5: Sub-bottom data (left) and corresponding sidescan image (right). Sidescan data are presented as uncorrected strips with sub-bottom profile data following the centreline of the sidescan data. Arrows point to the same locations on both panels. Depositional areas determined from the sub-bottom profile correspond to low backscatter on the sidescan sonograph. From Nitsche et al. (2004).

Seismic reflection or sub-bottom profiles

Seismic reflection and sub-bottom profiling can be used to map subsurface stratigraphy and structure, and define associated habitats (Greene et al., 1995). Sub-bottom profile images provide much more detailed images than seismic reflections, with energy received in the upper 50-100m. The detailed sub-surface reflections received allow much better correlation to acoustic facies, as illustrated in the above discussion with data from Nitsche et al. (2004). The upper reflections (upper 50 milliseconds) of the seismic data can also be used for acoustic facies mapping (eg. Rollet et al., 2001; Davis et al., 2002). Davis et al. (2002) achieved a good correlation between measured properties of the surface sediments (bulk density, porosity and mean grain size) and the reflectivity obtained from seismic sub-bottom profile data (Figure 6) across a range of siliciclastic environments. However, for carbonate sediments the geoaoustic behaviour is not as well understood, so it is not yet possible to make assessment of the sediment properties based on the acoustic signal across areas dominated by carbonate sediments (Davis et al., 2002).

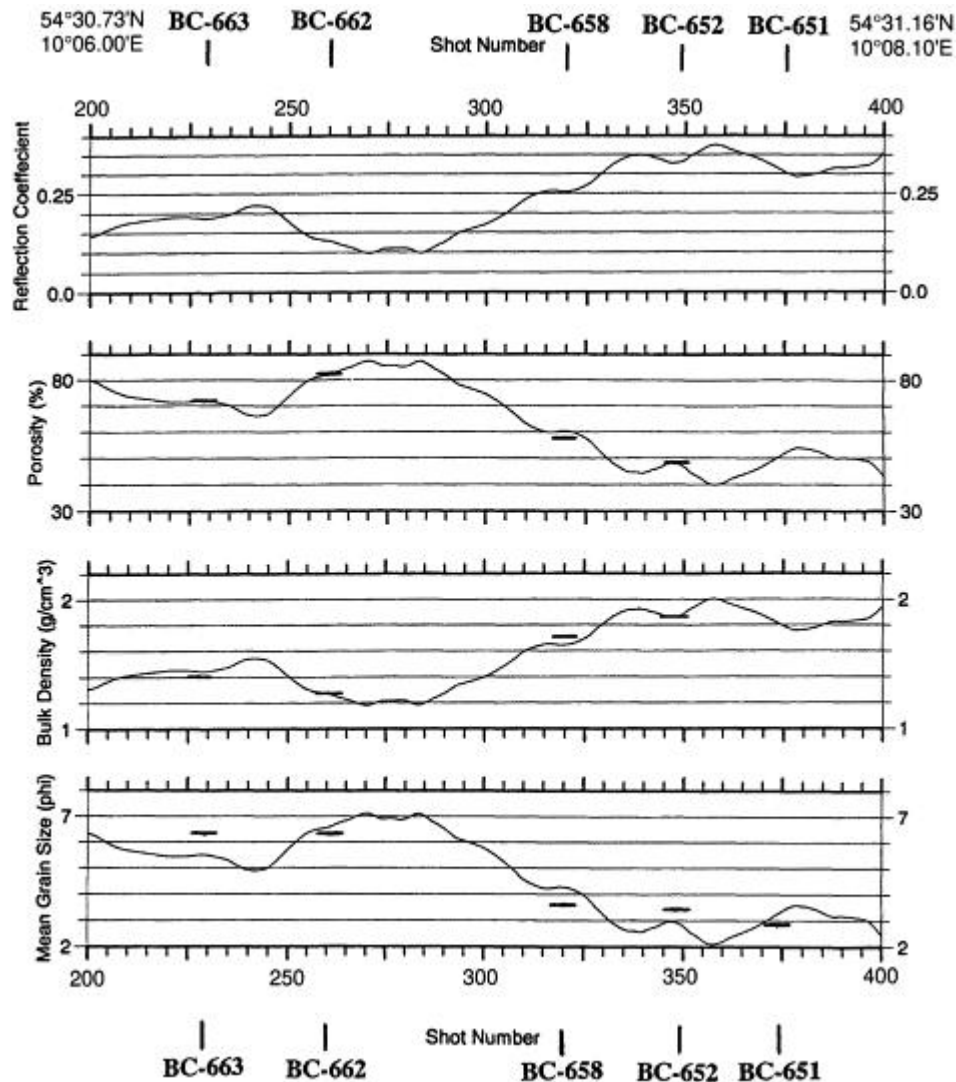


Figure 6: Sediment physical properties derived from seismic reflectance profiles calibrated against measured properties from box cores, Southern Baltic Sea (Davis et al., 2002).

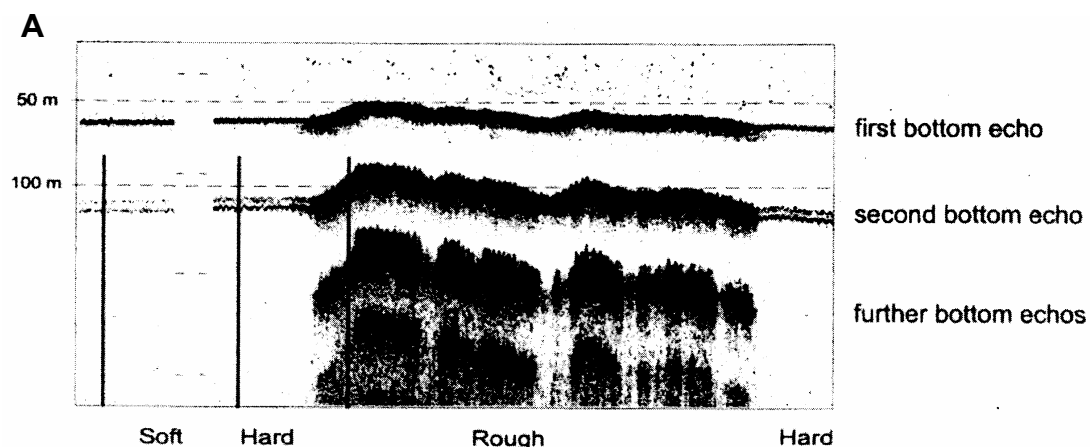
Acoustic facies

Acoustic return may be obtained from echosounders (single beam) and multibeam or swath sonar systems. Multibeam has the advantage over single beam systems of much greater areal coverage. The wider beam width of multibeam also allows the interpretation of cross track bathymetry, therefore allowing the backscatter to be corrected for changes in slope (Penrose et al., in press). Multibeam systems are, however, expensive and generally require larger vessels than single beam systems.

Echosounders are used primarily for measurements of water depth, however echograms can also be interpreted to determine changes in sea floor reflectivity and microtopography. Echo sounder data is increasingly being used to derive maps of hardness, softness and roughness (Figure 7; eg. Bax et al., 1999, Galloway, 2001, Kloser et al., 2001). Acoustic backscattering is affected by sediment size, sediment porosity, bulk density and surface roughness, with the acoustic energy decreasing with increasing sediment grainsize (Kloser et al., 2001). Other, more subtle, factors can also contribute to the acoustic signal, including the carbonate content, degree of compaction, depth and weather conditions (Whitmore and Belton, 1997).

Acoustic backscatter data in itself is insufficient to describe sediment properties without associated ground-truthing. Measurement of roughness and hardness, for instance, may be biased by high reflectivity and backscatter caused by even a small amount of shell material in the sediments (Penrose et al., in press). Biotic material above and below the sediment interface may also confuse the interpretation of the acoustic facies. The acoustic return from biotic material can be difficult to distinguish from the signal derived from the direct interface itself. These factors highlight the need for calibration of acoustic datasets.

Ground truthing of backscatter data can be done through either supervised or unsupervised methods (Galloway, 2001). The supervised method requires sediment type classes to be mapped prior to the survey, thereby “training” the system to detect known specific bottom types. This scheme does not allow post-processing of data to include previously undetected classes. The unsupervised calibration occurs post-survey. In this case, acoustic classes are derived following statistical processing. An example of this application is the Quester-Tangent software (IMPACT v3) which has been tested in Wallis Lake (NSW) (Ryan et al., 2004). This software transforms the echograms into Q-values using principal component analysis, and the values are then clustered into representative acoustic classes. Following classification of the acoustic data, the sampling program can be designed to target the defined acoustic classes (eg. Ryan et al., 2004). This unsupervised method of acoustic classification allows representative sampling of each class, therefore greatly increasing sampling efficiency.



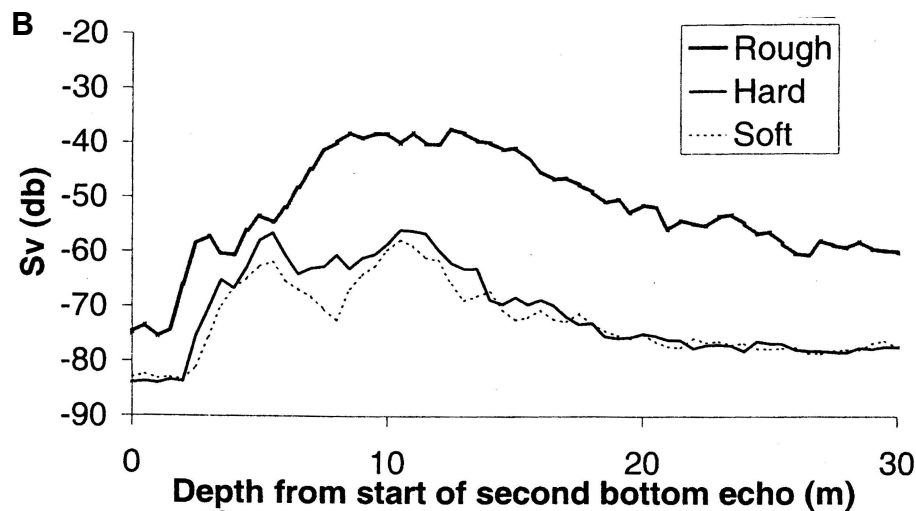


Figure 7: Example of the delineation of substrates from an echogram taken from Black Head, southeastern Australia (A), and the average backscatter energy of the second bottom echo which helps to distinguish between rough, hard and soft substrates (Bax et al., 1999).

Kloser et al. (2001) calibrated their interpretation of acoustic data by intensively sampling 10 reference sites with varying acoustics. Calibrations were based on the sampled benthic epi- and in-fauna, sediment samples, photographs and video. Simple indices of seabed roughness and hardness were derived from the acoustic data by applying the model of Orłowski (1984) and Heald and Pace (1996). The acoustic roughness and hardness indices showed general agreement to the seabed types determined from physical and photographic sampling. Successful definition of sedimentary environments have also been obtained from acoustic surveys in the Great Australian Bight (Rollet et al., 2001), with 7 acoustic facies identified matching distinct sediment types. Ground-truthing of acoustic facies (derived from 3.5 kHz and swath imagery) on the South Tasman Rise indicated that the distribution of acoustic facies is consistent with the major sedimentary processes of pelagic deposition and reworking (Whitmore and Belton, 1997). Some inconsistencies in the composition of facies on the South Tasman Rise and in other oceans (Figure 8) may reflect the water content in beds of uncompacted foraminiferal sand. Ground-truthing of acoustic classes in Wallis Lake also revealed some inconsistencies between the acoustic classes and sedimentological facies (Ryan et al., 2004). However, characteristic estuarine sediments such as marine sands and muddy basin sediments were clearly defined.

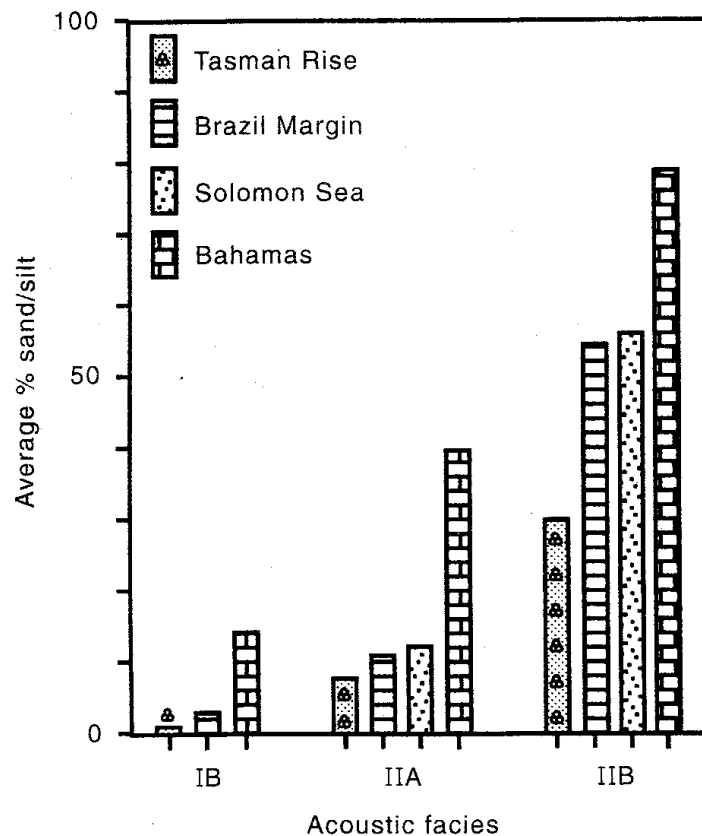


Figure 8: The varying percent interbedded sand/silt in acoustic facies from Tasman Rise, Brazil Margin, Solomon Sea and the Bahamas illustrates the effect of other factors on the echo type recorded on 3.5 kHz profiles. Whitmore and Belton (1997) suggest that water content in uncompacted beds of foraminiferal sand may be an important control on these echo-types. Figure from Whitmore and Belton (1997) and sources therein.

Discrimination of seabed features in the Australian South East Fishery were derived with three echosounder frequencies (120 kHz, 38 kHz and 12 kHz) and calibrated against sediment samples and seabed photography (Kloser et al., 2001). In this study, the 38 kHz transducer provided the best distinction for the soft-rough seabed character, but when imaged with the 120 kHz frequency, this facies merges with the hard-smooth seabed type. The 120 kHz frequency, however, had the best correlation to grainsize. The 12 kHz system had poor discrimination of surficial sediment data.

In the Gulf of Carpentaria, acoustic data collected with Simrad EK500 echosounder were correlated against measures of biodiversity and biomass (Hill et al., 2002). Highest biodiversity was found on transects with the highest hardness values. Areas of high acoustic hardness were also associated with high percentages of sand. In the Great Barrier Reef, the hardness-roughness categories derived from the acoustic remote sensing data were largely unrelated to species biomass data (Pitcher et al., 2002).

The application of each of the geophysical, seabed and visual sampling strategies is summarised in Table 1. This table also indicates the relevant scales for each technique and their limitations based on past studies. The regional scale techniques should be used to develop a strategy for local scale mapping to ensure that sample sites are

representative of each region. However, replicates should also be taken to measure finer scale variability. This is particularly important when attempting comparisons between point data (e.g. cores and grabs) and transects over 100's m from benthic sleds and trawls. Video should also be used to assess variability within the sample regions.

Sample collection

A wide range of techniques are used to obtain information about the biological and physical characteristics of the sea floor, which can help in groundtruthing geophysical datasets. All of these mechanisms provide qualitative information, but some also provide quantitative information. It is important to understand the limitations and applications of each these methods so that the data is applied appropriately in habitat mapping.

Dredge/benthic sled

A benthic sled is commonly used to collect samples of benthic organisms on the seabed. Sleds generally provide only qualitative information, but can be made at least semi-quantitative by standardising the condition and duration of towing (Gray et al., 1992). The benthic sled is typically comprised of a polypropylene 13mm stretched mesh attached to a 0.5 m high x 1.5 m wide metal frame, and this is lowered to the seabed and dragged along the bottom surface (Figure 1). Benthic sleds can not be used on hard, rocky substrates as this damages the net. On these hard-grounds, a rock dredge may be used to sample the benthic biota. The rock dredge typically consists of a rectangular metal collar to which a 1 m² chain bag is attached. The addition of a polypropylene liner can be used for consistency with the benthic sled in these environments. The rock dredge should not be used in areas of soft sediment since the short length of the net (typically ~1m) does not allow sufficient space to wash through fine sediment, resulting in clogging of the net. It is also important to optimise the drag time on the seafloor to ensure that the net does not become too full, as this can cause damage and loss of more fragile organisms.



Figure 1: Benthic sled. Photo by CSIRO.

The sled and dredge samples should be standardised according to the number of individuals (ie. species density) and mass (ie. biomass) per area sampled for consistency between sites and studies (eg. Thouzeau et al., 1991).

Beam trawls

The use of beam trawls on soft sediments provides qualitative to semi-quantitative information where the condition and duration of towing is standardised (Gray et al., 1992). There are various forms of beam trawls, but generally they consist of a long net, with the mouth held open by a rigid beam with metal runners at each end. The

bottom leading edge of the net is usually weighted downwards to prevent the upwards escape of mobile organisms. As with the benthic sled samples, data should be standardised to species density and biomass prior to analysis.

Grabs and cores

Grabs and cores provide quantitative information by sampling a known volume of sediment (Figure 2; Gray et al., 1992). Grab samples with low penetration should be rejected for faunal analysis to avoid underestimating the living infauna. At least 4 litres of sediment is required to obtain a representative sample for a 0.1 m² grab. A minimum of 2-3 replicates samples should also be taken for statistical analyses.



Figure 2: Smith-MacIntyre grab, photo by Geoscience Australia.

Sampling meiobenthos from grabs can be problematic as the surface sediments, where the meiobenthos is often richest, may be disturbed by down-wash as the grab approaches the sediment surface (Gray et al., 1992). The closing of the grab and its passage to the surface further disturbs the contents. A box sampler provides a better option for surface sampling (Figure 3), but the contents of this may also be disturbed if the top is not closed over adequately. In an analysis of infaunal communities in box core and multicore samples in the Weddell Sea region, Blake and Narayanaswamy (2004) found that the multicore collected between 12 and 83% more macrofaunal organisms than the box core. This study emphasises the importance of constructing box cores which do not produce a significant bow wave, as this can disturb the surface prior to sampling. Core samples are considered the best method for collecting and analysing a representative sample of the meiobenthos.

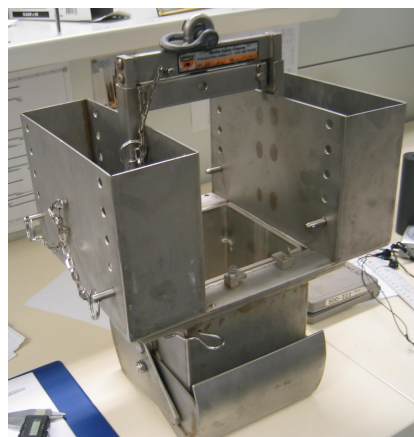


Figure 3: Box core (9-inch cube). Photo by CSIRO.

Diving

Diving is particularly useful in shallow water (above ~50 m), allowing detailed observations and in situ experiments to be set up (Gray et al., 1992). The main advantages of diving are that sample locations can be accurately determined, the surrounding substratum can be examined, and the representativeness of the sample assessed. Push cores may also be useful as these are often very successful in collecting undisturbed surface sediments. Diving is also one of the best ways of sampling hard substrates, where sleds and trawls can not be used. Diving is, however, time consuming and potentially dangerous, so video tows are better in situations where reconnaissance data are required.

Video/photography

With the reduction in cost and size, underwater video has become an integral tool for marine research (Figure 4). Underwater video has often been used to derive qualitative data for macro-species composition and abundance and has the advantage of providing a non-extractive sampling method. To obtain measurements of the size and volume of benthic biota, the correct calibration and photogrammetric methods must be utilised to correct for camera orientation, image reference and scaling (eg. Williams et al., 1998). The lens system must also be calibrated to correct for the change in the refraction index with changes in water temperature, salinity and density. ATV data has been used in conjunction with trawling and acoustic methods in the South Eastern Fisheries of Australia to derive measures of habitat roughness, percentage cover, species abundance and diversity, and the size of individuals (Wadley and Barker, 1996).

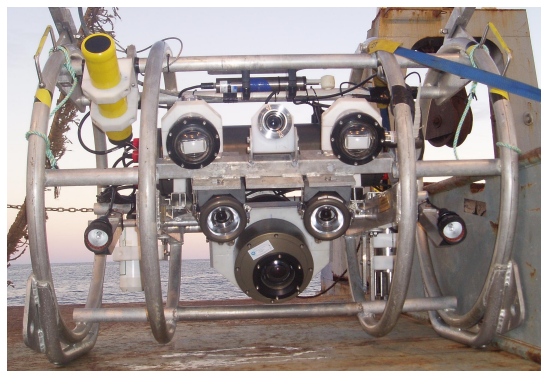


Figure 4: Towed underwater video operated by CMAR. Photo Mark Lewis (CMAR).

The addition of a high-resolution stills camera on the video frame allows much better identification of benthic fauna, and compared to grab samples significantly increases the speed of analysis and the data coverage. Video and photography are also particularly useful for estimating epifauna on hard bottoms which are difficult to sample, or for analysing the distributions of large, sparsely distributed organisms (Gray et al., 1992). The data can be categorised according to simple schemes, such as the semi-quantitative scale developed by Bax and Williams (2001) as follows: sparse (<25% cover); intermediate (25-50% cover); dense (>75% cover); clumps; individuals. A more sophisticated method has also been developed by CSIRO Marine and Atmospheric Research, with classification of substrates and biota on a coding basis (T. Wassenburg, pers.comm.).

Drawbacks of using underwater video or photography are that the benthic infauna are completely overlooked. This may lead to a gross underestimate of the benthic diversity since taxa such as bivalves and polychaetes will be undercounted (Kostylev et al., 2001). It is also rarely possible to identify organisms to species level. In a comparison of video and benthic sled sampling over the same sites, Pitcher et al. (2002) found that only 87 taxa were identified from the video (with 10-20% to species level), while nearly 1200 taxa were identified from the sled with ~90% to species level.

Sampling strategy

Sampling techniques such as cores, grabs, box cores and even benthic sleds provide a very localised picture of the seabed environment. It is important to determine the heterogeneity of sediments and habitats away from these points so that sampling can be conducted at an appropriate density. If sites are too close to each other the sampling will be inefficient, while sampling sites which are too far apart will provide inadequate information on the seabed features. Reconnaissance mapping using broad scale techniques such as acoustic backscatter, as well as video analysis can help to constrain relevant sampling scales. Intensive sampling in the Great Barrier Reef suggests that for this region the optimal sampling density is ~5-20 km with reliable habitat predictions only possible over scales of 5-10 km (Pitcher et al., 2002). Predictions which extrapolate beyond these distances will be highly unreliable.

Table 1: Summary of sampling techniques and their key applications and limitations over relevant spatial scales. Local scale typically 10's of km², regional scale extents over 100's km².

	Scale	Application	Limitations
Geophysical techniques			
Sidescan sonar	Regional	Determine sea floor morphology and composition	Some ambiguities in interpreting sedimentary features.
Echosounder	Regional	Measure seabed hardness & roughness	Need adequate ground truthing across different classes. Coverage limited.
Seismic profiles	Regional	Subsurface stratigraphy, structure and sediment properties. Helps to constrain acoustic signal.	Coverage limited.
Multibeam swath	Regional	Detailed bathymetric mapping	Beam width limited in shallower waters (current system allows a max beam width of 7 x water depth)
Seabed sampling			
Grab	Local	Surface sediment composition, quantify living and fossil micro- and meiofauna	Need to sample replicates to ensure representativeness
Core	Local	Surface and down core sediment composition, quantify living and fossil micro- and meiofauna	Need to sample replicates to ensure representativeness
Benthic sled	Local	Quantify living macrofauna density and biomass	Cannot sample effectively on hard grounds, may cause unreasonable damage in highly protected areas
Benthic trawl	Local - Regional	Broader scale sampling of living invertebrates and fish	Should be used in conjunction with sled data as these sample very different parts of the ecosystem.
Visual methods			
Video	Local	Non-extractive, non-quantitative, determine major invertebrates and sea floor morphology	Non-quantitative for biological assessments. Species ID to higher levels only, underestimates infauna.
Diving	Local	Shallow water only, representative sampling possible, determine structure & patchiness of communities, macrofaunal composition.	Limited to shallow water (<50 m), potentially dangerous.

Biological analyses

Fauna

The benthic fauna can be subdivided into microfauna, meiofauna, macrofauna and megafauna, in increasing order of size. The size divisions between each of these classes are fairly arbitrary, varying between researchers. The macrofauna, and particularly those from soft-bottoms, are the most widely used component for environmental impact studies (Clarke and Warwick, 2001). There are several advantages to using the macrofauna: 1) they are not very mobile, so useful for studying the effects of pollutants; 2) their taxonomy is relatively easy; 3) quantitative sampling is relatively easy; and 4) there is extensive research literature on the effects of pollution and this can form the basis for evaluating case studies. Limitations of using macrofauna include: 1) a relatively large volume of sediment must be collected, requiring large research ships; 2) processing of the samples is labour intensive and time consuming, and the bulk of it must be done at sea; and 3) the response of macrobenthos to changes in the environment is slow, so full establishment of a community characteristic of the new environment may take several years.

The meiobenthos also share the advantage of limited mobility, and are therefore also useful for studying local scale effects. Other advantages include: 1) their small size and high density in marine sediments which makes quantitative sampling easy; 2) the small volume of sediment collected can easily be transported back to the lab for processing; and 3) they have short generation times, on the order of months, so their response to environmental change should be reflected in the community more quickly. Disadvantages include: 1) their taxonomy is generally difficult; and 2) community responses of the meiobenthos to disturbance or pollution is not well documented.

Studies in which both the meiofauna and macrofauna have been analysed invariably show different distribution patterns between the two groups for univariate measures such as diversity (see review in Warwick and Clarke, 1991). Analysis of the overall community structure, through multivariate techniques, indicates much greater correspondence between distributions of the meiofauna and the macrofauna, revealing the greater sensitivity of multivariate analyses.

Various approaches are taken in the analysis of species abundances. A range of taxonomic groupings may be applied, and counting may be as presence/absence, total or relative abundance, or biomass. Presence/absence data is the simplest level of counting applied, and this technique has previously been demonstrated to be effective for classification of benthic samples (Field, 1970; Moore, 1974; Moran, 1981; Long et al., 1995). Long et al. (1995) used presence/absence data for macrofauna collected in beam trawls in the Gulf of Carpentaria since this avoided uncertainties regarding what constituted an individual. Their counts included plants (seagrasses and algae) as well as solitary and colonial animals which meant that it was not always possible to count individual members of a species.

Prior to statistical analysis, rare species should be removed to reduce the number of chance co-occurrences of rare species. Stations which have very low total abundance should also be removed (Thouzeau et al., 1991). Removing rare species has been shown to have little effect on the outcome of the analysis (Stephenson and Cook, 1980). Long et al. (1995) restricted their analyses to species found at more than 2 stations. Alternatively, all rare species may be combined for each station, under

categories of “number of singletons” for those species occurring at only a single station, and “number of uncommon” for those occurring at 2, 3 or 4 sites (Pitcher et al., 2002). This allows examination of any parameters which may lead to these rare species occurrences.

Taxonomic levels

It is not always possible to identify taxa to species level as many marine benthic organisms remain undescribed. Several studies with species-level data have compared the results of their analyses at various taxonomic levels to assess the most appropriate level of identification (Warwick, 1988; Olsgard et al., 1998; Clarke and Warwick, 2001; Kostylev et al., 2001; Pitcher et al., 2002). Olsgard et al. (1998) compared correlations to species matrices for macrofauna also identified to genus, family, order, class and phylum for several different datasets with pollution gradients. This study indicated close correlations to the species matrix for genus and family, with lower correlations at taxonomic levels higher than order. Kostylev et al. (2001), Gray et al. (1990), Warwick and Clarke (1991) and Warwick (1988) also found that there was a negligible loss of information between species and family level data. Warwick (1988) suggests that higher level taxa may more closely reflect gradients of contamination than those based on species abundances, since species are more affected by natural environmental variables.

Results from a study of benthos across natural gradients in the Great Barrier Reef are also consistent with those across pollution gradients. The distinction between habitats based on species level data is lessened when identification is made to family level, and is severely degraded at class and phylum level (Figure 8) (Pitcher et al., 2002). Two thirds of the spatial information established from species level data was lost when species were resolved at the level of Class. Species data allows the highest level of distinction between benthic habitats, and therefore forms the strongest basis for predicting biophysical relationships. An additional technique explored in this study was the differentiation of habitats from video and acoustic data. These two techniques have a very low correlation to the species level data due to the difficulty of identifying, observing and quantifying the benthos (Figure 9).

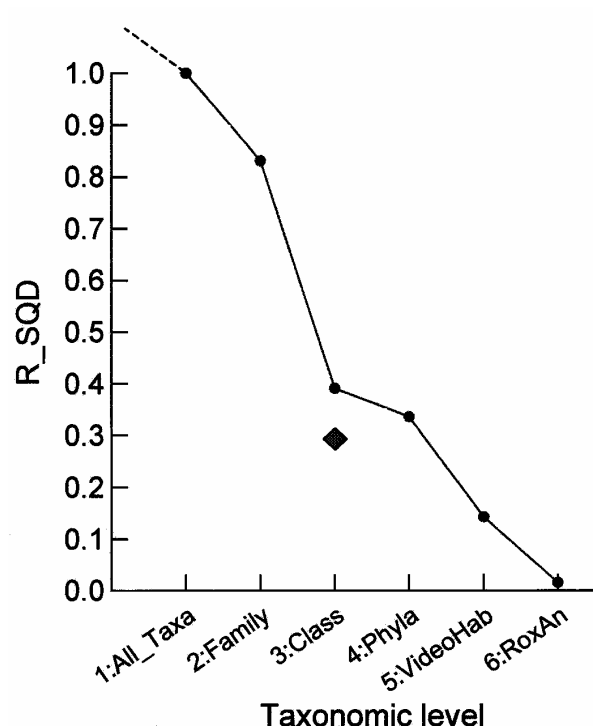


Figure 9: The loss of seabed biodiversity information with progressively coarser taxonomic levels is indicated by the R-squared correlation for the Bray-Curtis dissimilarity matrices relative to distribution patterns at the species level (Pitcher et al., 2002). The R-squared value for the Class presence-absence data is indicated by the diamond. Video habitat and RoxAn (acoustic) data indicate low taxonomic resolution, with a poor relationship to species level patterns.

Functional groups and community structure

Assigning organisms to functional, feeding or morphological groups can provide additional information about community structure and environmental associations. This approach is particularly useful when there are many undescribed taxa. Morphological characteristics for bryozoans may include characteristics such as soft, fenestrate, and massive (Bax et al., 1999). Bone et al. (1993) recognised 9 different morphologies amongst bryozoans on the Lacepede Shelf, southern Australia. This study showed that the distribution of each morphotype was related to the characteristics of the environment, in particular the water depth (and associated changes in nutrient supply, water temperature and bottom current energy) and the sediment grain size and mineralogy. Evidence from video transects in southeast Australia also indicate that the form of invertebrates is distinct between habitat types (Bax et al., 1999). In soft habitats sponges, bryozoans and ascidians are soft and flexible, while the transition to hard and rough environments is associated with increasingly firm and dense types of sponges and bryozoans, with solid anchor points. Since sessile benthic organisms are spatially fixed, the substrate conditions are critical to their survival and proliferation (Kostylev et al., 2001).

Feeding modes have also been widely linked to sediment types (eg. Long and Poiner, 1994; Long et al., 1995; Kostylev et al., 2001; Denisenko et al., 2003), particularly deposit feeders. Deposit feeders, as the name suggests, ingest large volumes of sediment which provide nonliving organic matter which can be digested directly, bacteria, bacterial products, living microscopic plants and animal matter (living or

dead) (Jumars, 1993). A relationship between deposit feeders and grain size distributions has been suggested on the basis that small particles have high surface-to-volume ratios and therefore provide high amounts of digestible material per unit volume of sediment. Results from experimental studies mostly support this theory of particle size selection, but they are not conclusive (Taghon, 1982). The grouping of organisms as suspension or deposit feeders is also not as clear as once thought. Some studies have found that a number of deposit-feeders living in muddy sediments will suspension-feed in response to suspended sediment flux (Taghon et al., 1980; Levinton, 1991). Additionally, some species once thought to be suspension-feeders actually utilise deposited sediment as well (Mills, 1967; Tenore et al., 1968; Hughes, 1969).

Another approach to characterising community structure is to determine the function of various species within the community. Williams and Bax (2001), for instance, describe community structure in fish based on four levels: dominant species; typical species; discriminating species; and restricted species. The dominant species is that with the greatest mean biomass and total raw biomass, while typical species are identified as those that contribute most to the similarities within groups, and discriminating species are those that contribute most to dissimilarities between groups. Restricted species were defined as those occurring only within one community. In this study of the fish community structure, these categories were overlain on seabed types to produce a biophysical map, which revealed some close associations between fish communities and the substrate. However, factors such as depth and the local hydrography were also shown to be important in determining community distributions.

Abundance, biomass and density

For varying sample sizes, abundance data cannot be compared directly between sites. In these cases species density should be used, measured as the number of individuals per area sampled (eg. Thouzeau et al., 1991). Biomass data can provide additional information regarding the size distributions and relative productivity of communities. This is measured as the mass of the biota over the area sampled. The use of the wet weight measure will, however, tend to favour taxa that contain large amounts of water, such as poriferans and ascidians, over taxa with little water content, such as bryozoans (Ward et al., in press).

Comparison between species abundance and biomass can provide useful insight into community structure and evidence of disturbance. Sites which have suffered disturbance tend to be dominated by a large number of species with small biomass, while an undisturbed community is dominated by only a few species with large biomass (Clarke and Warwick, 2001).

Measures of diversity

Measures of diversity are useful as a way of summarising complex assemblage data into a single index, though they are less sensitive than species data for detecting community change (Clarke and Warwick, 1991). There are many diversity measures, but most of these tend to be different combinations of the same two factors: the number of species and the total number of individuals. The most common indices are summarised here.

One commonly used index is the **Shannon-Wiener diversity index**:

$$H' = -\sum_i p_i \log(p_i)$$

where p_i is the proportion of the total count accounted for by the i th species. One drawback of this index is that it varies according to sample size (or the total number of species), so it can not be used to make comparisons between samples (Legendre and Legendre, 1984). Measures of species richness are also very dependent on the sample size as they are often given simply as the number of species in a sample. The **Margalef index** (d), however, does also incorporate the total number of individuals in the sample (Clarke and Warwick, 2001):

$$d = (S-1) / \log N$$

where S = total number of species

N = total number of individuals

The influence of sampling effort on the number of species observed is shown in Figure 10.

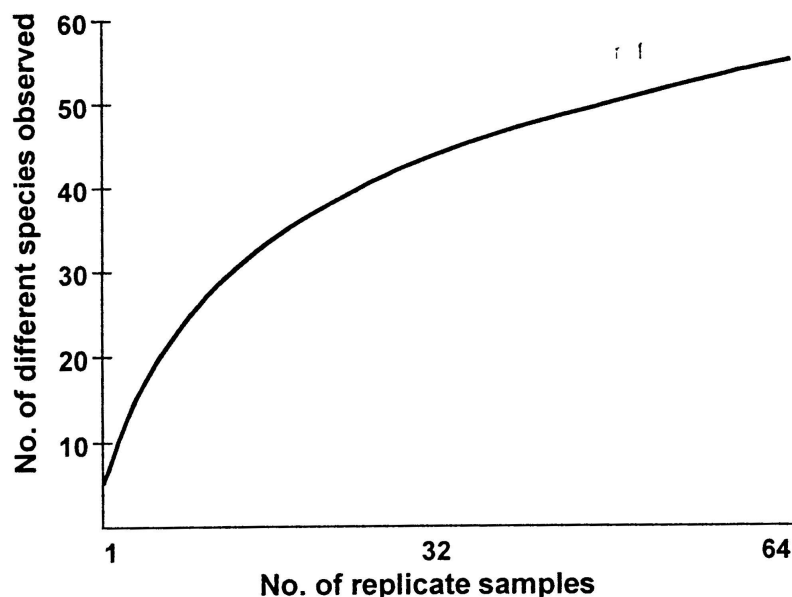


Figure 10: The number of species observed versus the number of replicate samples (Clarke and Warwick, 2001). The number of species increases with the number of observations.

Pielou's evenness index (J') expresses how evenly individuals are distributed among the different species, or their equitability (Figure 7; Clarke and Warwick, 2001). This index incorporates the Shannon diversity value to determine the proportion of this to the maximum possible value, in other words, the value that would be achieved were all species equally abundant:

$$J' = H' / H'_{max} = H' / \log S$$

where H' = Shannon diversity index

S = total number of species

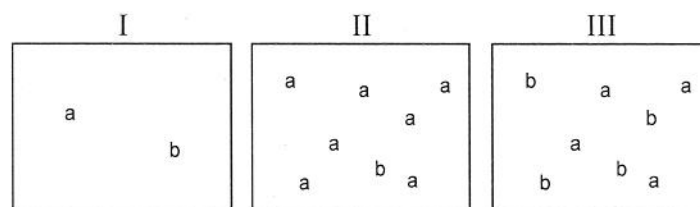


Figure 8: Changes in evenness for 3 samples composed of species a and b (Pitcher et al., 2002). All three samples have a species richness of 2, but there are differences in evenness. Sample III has the highest evenness, while sample II has low evenness (or high dominance).

The **Simpson index** measures dominance, with largest values corresponding to assemblages dominated by one, or very few species (Clarke and Warwick, 2001). The index measures the probability that two individuals taken at random from a sample belong to different species. The Simpson index is the least sensitive of the indices to changes in sample size. There are a variety of forms of this index, with the last two appropriate when the total sample size (N) is small:

$$\begin{aligned}\lambda &= \sum p_i^2 \\ 1 - \lambda &= 1 - (\sum p_i^2) \\ \lambda' &= \{\sum_i N_i(N_i - 1)\} / \{N(N - 1)\} \\ 1 - \lambda' &= 1 - \{\sum_i N_i(N_i - 1)\} / \{N(N - 1)\}\end{aligned}$$

N_i is the number of individuals of species i , p_i is the proportion of species i in the total count, λ represents the sample dominance, while its complement, $1 - \lambda$, represents the evenness.

Other measures developed by Warwick and Clarke (1995) are indices for taxonomic diversity and distinctness. These indices are based both on the species abundances (x_i) and the taxonomic distances (ω_{ij}) between every pair of individuals (from species i to species j). The total sample size (N) is also included. The taxonomic distance between two individuals of the same species is zero, one for the same genus but different species, and two for different genera but the same family. The average **taxonomic diversity** (Δ) is defined as follows:

$$\Delta = [\sum \sum_{i < j} \omega_{ij} x_i x_j] / [N(N - 1)/2]$$

The taxonomic diversity is the expected path length between any two individuals chosen at random, and is essentially an extension of the Simpson index. The **average taxonomic distinctness** was developed to remove the dominant effect of the species abundance distribution $\{x_i\}$, leaving a measure which better describes the taxonomic hierarchy. This index has the following form:

$$\Delta^* = [\sum \sum_{i < j} \omega_{ij} x_i x_j] / [\sum \sum_{i < j} x_i x_j]$$

In summary, this index describes the expected taxonomic distance apart of any two individuals chosen at random, providing the two individuals are not from the same species.

Species-environment relations

Key associations

Relationships between benthic organisms and their environment have been tested in a variety of settings. Many of these studies invoke a relationship between grain size and species distributions (eg. Thouzeau et al., 1991; Long and Poiner, 1994; Somers, 1994; Greene, 1995; Auster and Langton, 1999; Kostylev et al., 2001; Post et al., submitted manuscript). The sedimentary environment may provide important features for species refuges and habitat. Crevices or interstices between cobbles and boulders may provide shelter, hard surfaces allow a substrate on which epibenthic organisms can grow, and boulders and sand waves can provide shelter from currents (Auster and Langton, 1999). Mixed biogenic sediments have also been shown to provide a diversity of habitats and therefore of organisms (eg. Webb et al., 1976; Thouzeau et al., 1991; Kostylev et al., 2001). The mixture of sand, gravel, cobble and bryozoan

fragments on eastern Georges Bank were suggested as providing a heterogeneous habitat and refuge for a high diversity of invertebrate species (Kostylev et al., 2001). In some regions the organic carbon content is correlated to grain size (Figure 11; Mayer, 1989), suggesting that this may be an additional mechanism for associations between species and the sedimentary environment.

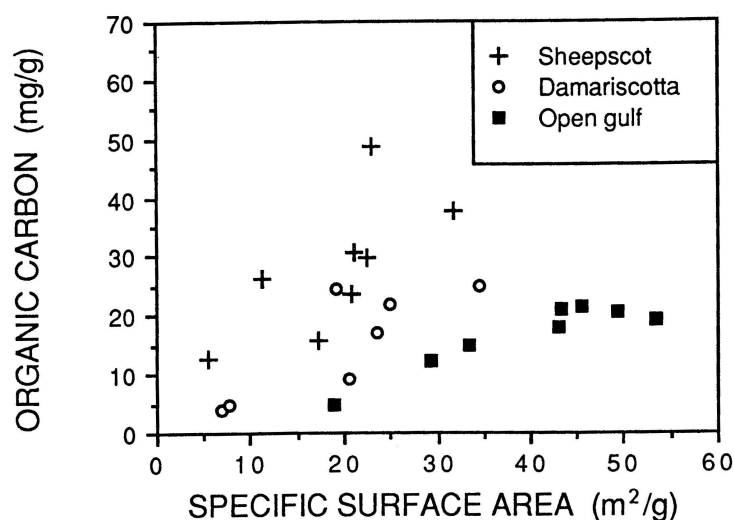


Figure 11: Relationship between organic carbon content and mineral specific surface area in the Gulf of Maine (Mayer, 1989).

Surface sediments will retain the skeletal remains of specimens, providing an additional insight into the community composition, and the possibility to track these changes through time. The distribution of benthic foraminifera against a suite of physical parameters in Torres Strait sediments is similar to the relationship exhibited by the preserved microbiota (Post et al., in press). This result emphasises the potential for the fossil content to delineate habitat conditions through space and time. However, soft bodied specimens or those with only small skeletal elements will be under-represented in the sediments compared to their abundance in the living assemblage. Ward et al. (in press) compared the sedimentary facies and the living epibenthic assemblage in the Great Australian Bight, and found significant differences in the dominant species represented in each data set, due to the under-representation of poriferans and ascidians. The utility of the fossil record is, however, shown by a study of benthic foraminifera in a small number of samples from the Gulf of Carpentaria (Post et al., submitted manuscript). The diversity of the benthic foraminifera shows a good correlation to the diversity of living macrofauna, with and even stronger correlation found from the combination of foraminiferal diversity, organic carbon flux and water depth.

Relationships between organisms and environmental parameters are also dependent on scale. In a study of macrofaunal distribution, Ramey and Snelgrove (2003) found that grain size had an important influence on community composition. On a broader scale, however, community composition was most strongly (negatively) associated with the sedimentary organic carbon content. Yet, larger scale studies have shown a positive relationship between surface production and benthic biomass and/or abundance (eg. Grebmeier et al., 1988; Ambrose and Renaud, 1995). These relationships also vary between regions. In the Gulf of Carpentaria, Burford et al.

(1994) found that organic carbon was of secondary importance to sediment type in describing the distribution of macrobenthos.

Another factor which has been shown to be important in determining interactions between benthos and the sedimentary substrate is the age of the sediments and their relation to modern hydrodynamic processes (Webb et al., 1976). Relict sediments which are no longer in hydrodynamic balance create a very different environment to sediments which are in hydrodynamic balance and have a similar grain size. Recently deposited muddy sediments, for instance, tend to have high water content, and organisms are predominantly deposit feeders and burrows are unstable. Relict muddy sediments, by contrast, are hard, organisms are predominantly suspension feeders and there are many permanent burrows. Defining the modern processes is therefore a crucial aspect of defining the marine sedimentary environment.

The stability of the sediment, rather than particle size itself, may be of greater importance in controlling the community structure of benthic organisms (Newell et al., 1998). Currents, for instance, play an important role in defining sediment grain size (eg. Jumars, 1993; Wildish and Kristmanson, 1997), and also control the distribution of larvae (Snelgrove and Butman, 1994). The distribution of larvae in relation to a particular grain size may therefore reflect their passive sorting by currents, rather than selective preference. Complex shear forces at the sediment-water interface also control factors such as food availability, and pore water flow (Newell et al., 1998). Granulometric properties alone are therefore unlikely to account for the distribution of animals in most sedimentary habitats. A study in the English Channel concluded that granulometric properties of the sediments are likely to account for a maximum of 45% of the variability found in the biological component (Newell et al., 1998). Analysis of the relationship between biota and physical properties will need to take into account factors such as water depth, temperature, light intensity and food supply in addition to the nature of the substrate (Mayer, 1989; Murray, 1991; Blaber et al., 1994; Hill et al., 2002).

The importance of the energy of the substrate is illustrated by patterns of diversity around a reef in the Gulf of Carpentaria (Post et al., submitted manuscript). Samples collected on the active talus slope had extremely low diversity compared to surrounding areas with much lower sediment input. The species composition and biomass distribution was also distinct, with suspension feeders dominant, composed almost exclusively of solitary anemones with a very low biomass compared to other sites where they were present. Sediment input at this site was composed of sand-sized reworked reef sediments. The low biomass at this site suggests that there was low food supply delivered in these reworked sediments, limiting the biological productivity.

The relationship between organisms and physical parameters varies between taxa, and organisms exhibit different sensitivities to their environment. In the Great Barrier Reef, 50-65% of benthic species had a predictable response to environmental gradients, while others were more widely distributed (Pitcher et al., 2002). In the Gulf of Carpentaria, different taxa have varying responses to the environmental variables. Abundance and species richness of benthic infauna largely follow sediment grain size trends (Long and Poiner, 1994), with more recent studies also revealing the importance of oxygen and temperature (Hill et al., 2002). Demersal fish are most

strongly associated with water depth (Blaber et al., 1994; Hill et al., 2002), which is probably also a reflection of temperature. The reef-associated fish have a more restricted distribution, pointing to the potential importance of sediment type, benthos or benthic structure on these species (Blaber et al., 1994). Prawn species in the Gulf show significant correlation to both depth and mud content (Somers, 1994). These factors explain nearly 40% of the variance in the distribution of the two tiger prawn species, with increasing abundance associated with decreasing water depth and increasing mud content. Depth and sediment type also influences the distribution of the endeavour and banana prawns.

Feeding modes of the benthic infauna in the Gulf of Carpentaria seem to show some association with sediment grain size, however, patterns of individual organisms do not necessarily match those of the community as a whole (Long and Poiner, 1994). For instance, the highest proportion of deposit feeders occur in sediments with high mud content, yet their greatest abundance is associated with decreasing mud content. The proportion of suspension feeders is positively correlated with increases in sand and gravel content, while their abundance increases only with increases in sand content. On the whole, abundance, biomass and species density also decrease in deeper waters, independently of grain size.

Indicators of disturbance

The response and recovery of benthic organisms to disturbance is an important area of research, particularly in regions of intensive fishing. Benthic communities in the Northern Prawn Fishery of Australia (which includes the Gulf of Carpentaria) have been noted to be at potential risk due to prawn trawling, resulting in management measures to protect them (Northern Prawn Fishery Management Advisory Committee, 2003). Otter boards and groundchains on the trawls skim over the seabed to stimulate the prawns and cause them to rise into the mouth of the trawl. However, up to 450 vertebrate species and 230 invertebrate species have been caught incidentally as bycatch. Sedimentary features are also damaged by trawling through the smoothing of sedimentary bedforms, a reduction in bottom roughness and by altering the subsurface sediment fabric including habitat structure such as burrows (Auster and Langton, 1999; Collie et al., 1997).

The vulnerability of a habitat to disturbance is a function of its resistance to modification from a particular source, and its resilience, or the time taken for the habitat to resume its original ecosystem functions once the modifier is removed (Bax and Williams, 2001). The vulnerability of a habitat varies depending on its characteristics (Figure 12). The restoration of storm produced sedimentary features, for instance, depends primarily on the grain sizes of the sediment and depth to which storm-generated surge and currents occur (Auster and Langton, 1999). Some features, particularly fine-grained deposits, will reform following seasonal or annual storm events, while sand and gravel environments will require larger scale events, occurring on decadal or longer time scales (Newell et al., 1998; Auster and Langton, 1999).

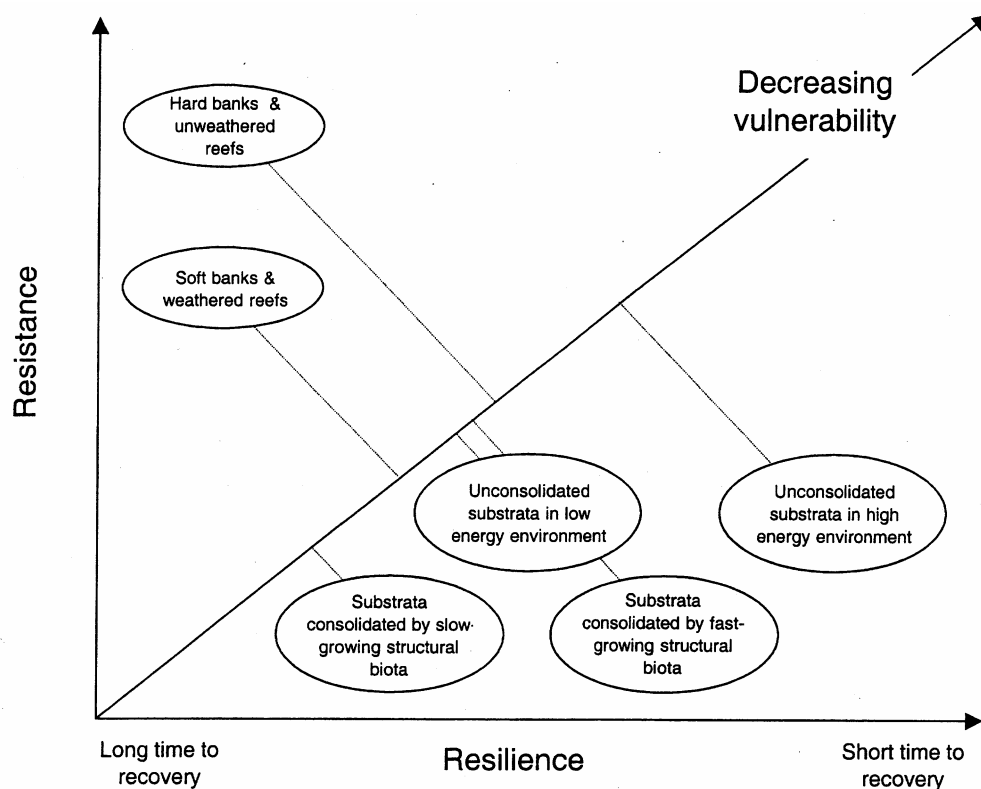


Figure 12: The vulnerability of generalised substrate types is a function of their resistance to physical modification and their resilience once modified (Bax and Williams, 2001). This figure illustrates the vulnerability of the substrate as influenced by sediment consolidation, morphology, the energy of the environment and the biological structure.

The recovery of the benthic community itself also depends on the relative frequency and intensity of the natural physical disturbances that influence it. A benthic habitat in regularly disturbed areas (eg. the surf zone), may be relatively invulnerable to physical disturbances if they are within the normal range of frequency and intensity (Bax and Williams, 2001). By contrast, small physical modifications to habitats at greater depths than those where storm events penetrate may require a long time before the community is re-established. The recovery of a species also varies depending on its life cycle. Sponges, for instance, are particularly sensitive to disturbance because they recruit aperiodically and are slow growing in deeper waters (Reiswig, 1973; Witman and Sebens, 1985; Witman et al., 1993). Many other species, including hydroids and ampelescid amphipods, reproduce once or twice a year, so may recover more quickly.

The impact of disturbance on community structure is illustrated in Figure 13. Following disturbance which has caused obliteration of the previous community, opportunists will colonise the new habitat, and these tend to have very high abundance but relatively low biomass and species diversity (Newell et al., 1998; Clarke and Warwick, 2001). The opportunists will generally decrease once additional, larger species begin to invade. During the transitional phase there is high species diversity, with diversity eventually decreasing as the equilibrium community is established, comprising larger, long-lived and slow growing species. The time required for each phase varies between sediment types, climate and hydrographic

conditions. Colonisation is relatively rapid in areas of strong currents compared to areas of low current velocity (van der Veer et al., 1985), and longer recovery times are reported for sand and gravels (Kenny and Rees, 1996) relative to fine-grained deposits such as estuarine muds where frequent disturbance produces long-lived communities (Ellis et al., 1995). Colder waters also typically require longer recovery times than warmer areas due to the typically large slow-growing species at high latitudes (Newell et al., 1998).

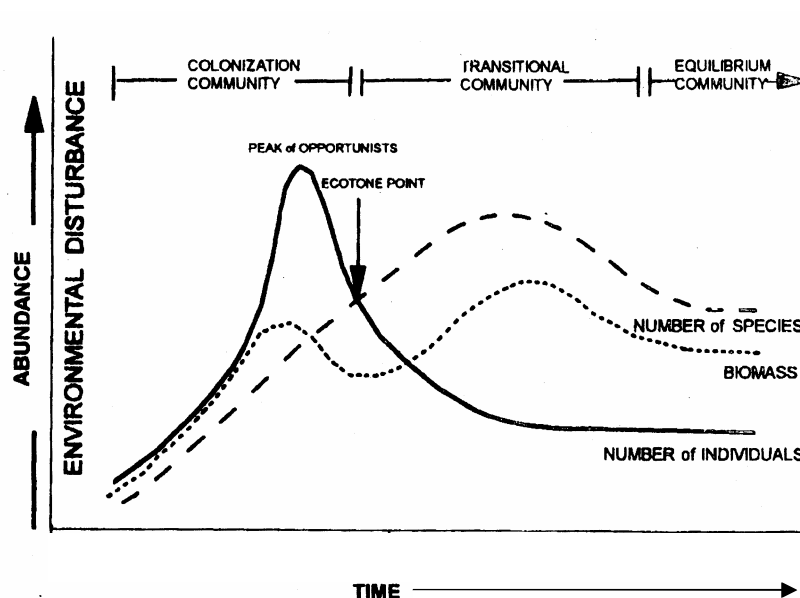


Figure 13: Schematic diagram showing the change in community structure from the initial colonisation following disturbance, to the transitional community and then the equilibrium community (Newell et al., 1998).

The responses of organisms to pollutants and seabed disturbance has been shown to vary between the macrofauna and meiofauna, with meiofaunal abundance, biomass and diversity showing little change following disturbance (Warwick et al., 1990). The difference in their response is thought to reflect the different habitat requirements of these two groups. Meiofaunal diversity is probably less sensitive to changes to the sediments since these organisms actively seek out food particles, and each species consumes particles of preferred size, shape and quality. Macrofauna, by contrast, are relatively unselective in their feeding habitats, and this means that they depend on the spatial variability of the habitat to maintain their diversity. Instability of the sediments may therefore cause a marked reduction in macrofaunal diversity.

In studying disturbance it is important to hold variables such as depth and grain size constant by sampling at constant depth or within a narrow range of grain sizes (Gray et al., 1992). If this is not possible, it is important to sample at control sites which have physical variables that match those at the impacted sites.

The application of benthic habitat mapping

The integration of physical and biological datasets forms the basis for benthic habitat mapping. This characterisation of habitats is crucial for better management of biological and economic resources. For Australia's Southeast Regional Marine Plan, detailed bathymetric mapping by Geoscience Australia revealed a diversity of habitats, including the Tasmanian Seamounts (now set aside as a reserve) and the

Murray Canyons (National Oceans Office, 2001). Subsequent biological sampling of the seamounts lead to the discovery of a biologically diverse and unique ecosystem with 850 species sampled, about a third of which were new to science.

As part of the development of the Northern Regional Marine Plan, 15 bioregions have been identified for the area on the basis of climate, oceanography, geology, geomorphology, biota and estuaries (Hill et al., 2002). A recent analysis of the sedimentology and geomorphology of the region by Heap et al.(2004) will form a key component of the final regionalisation, since there is currently insufficient biological data to fully characterise the habitats. Recent surveys by Geoscience Australia and CSIRO Marine Research in the region will allow more rigorous testing of surrogates which can be used to predict biodiversity and community composition throughout this area.

Benthic habitat mapping has also proved successful in the better management of fisheries. On Browns Bank Canada, for instance, maps of bathymetry, backscatter strength, surficial geology and benthic habitat were provided to the scallop industry, with immediate benefits to both the fishing industry and the environmental protection of the area (Pickrill and Todd, 2003). In just one year, the time spent dragging the seabed by the fishers was reduced by 75%. This had huge economic benefits to the fishing industry while also reducing the environmental impact. Knowledge of the bottom-type allowed lighter scallop rakes to be used, reducing benthic disturbance, and areas of sensitive habitat or those areas devoid of scallops could also be avoided.

Summary and Recommendations

There is still much to be learnt regarding the distribution of benthic fauna with respect to physical variables, but in areas where we have sufficient data to integrate these datasets there are significant gains for marine management (eg. Pickrill and Todd, 2003). In the Australian context we will soon be well-placed to integrate physical and biological data sets for the Northern Planning Region, with the recent data collected during surveys in the Gulf of Carpentaria and Arafura Seas during February to May 2005. However, even with these recent surveys there are vast areas of the northern region which remain unsampled, particularly in terms of the benthic biota. A key part of the current data analysis will be determining physical surrogates for biological diversity, and applying these results to guide further sampling and possibly conservation efforts. Other areas of Australia's marine jurisdiction (apart from the south east) require further sampling to define benthic habitats.

There are several recommendations arising out of this review which should be applied in future research. The methods should be employed across the relevant scales of analysis, and with regard to the application of the project.

- Reconnaissance mapping using multibeam bathymetry and associated backscatter components should be used to target samples at relevant spatial scales, and to capture the maximum degree of substrate variability in biological and sediment analysis. This approach will allow much better testing of the relationship between physical and biological distributions.
- Acoustic mapping must be adequately ground truthed with seabed sampling and photography. A combination of acoustic techniques can also aid interpretation, eg. sidescan or multibeam sonar in combination with sub-bottom or seismic profiles.

- Different sampling techniques have different strengths and weaknesses. It is therefore important to use a combination of methods for sampling both the benthos and the sediments. These techniques include benthic sleds (for sampling macrofauna), grabs, box cores and gravity cores (for analysis of meiofauna and sedimentary composition) and video for qualitative assessment of the habitats and finer scale heterogeneity. Video is particularly useful on rocky grounds, where sampling devices are more difficult to deploy.
- To ensure that grab and core samples are representative, a minimum of 2-3 replicates should be taken at each site, particularly where detailed biological analysis will be undertaken.
- For detailed habitat mapping biological samples should be identified to species level, but at the very least to genus or family level. This allows much greater predictive power for defining physical surrogates.
- Diversity measures should be used in combination with other measures of community structure since diversity alone is not sensitive enough to detect differences in benthic community structure.
- Measurements of grain size need to be combined with data relating to seabed stability and the age of the sediments. This will allow an assessment of the hydrodynamic balance of the sediments.
- Habitat vulnerability should be assessed in terms of both natural and human disturbance. The effects of human disturbance will depend on the frequency of natural disturbances which can regenerate physical structures removed by processes such as trawling. Communities which experience frequent natural disturbance may be less susceptible to human disturbances, but their recovery will also depend on the life cycle of the organisms.

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