

SPECIAL TOPIC

Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100–1100 m depths)

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Abstract

The first large systematic collection of benthic invertebrate megafauna from the Australian continental margin (depths > 100 m) revealed high species richness and novelty on the south-western continental slope (~100–1100 m depth; ~18° S–35° S). A total of 1979 morphologically defined species was discriminated in seven taxa across all samples: Demospongiae, Decapoda, corals (Octocorallia and Antipatharia), Mollusca, Echinodermata, Ascidiacea, and Pycnogonida. Collectively, 59% were estimated to be new or unnamed species. The distribution pattern of megafaunal communities, analysed with a suite of 17 physical covariates, was most influenced at large spatial scales (>100s km) by bottom temperature, oxygen concentration and latitude, whereas at smaller scales (10s of km), seabed type was most influential. Many covariates are driven by the same physical processes and are correlated (e.g. to depth or latitude), thus it is not possible to ascribe causal relationships to fauna distributions. However, their identification highlights the spatial scales that determine the composition of megafaunal communities. Regional-scale transitions in bottom temperature and oxygen concentration are determined by water masses and currents that interact with the south-western margin seabed in different ways depending on location. The nested, smaller-scale heterogeneity of seabed type, classified simply as 'hard' or 'soft' terrain, differentiates consolidated attachment sites for sessile fauna from sediments suited to mobile and burrowing fauna. Different physical factors affect the distribution of benthic fauna at different scales. Collectively, these patterns of heterogeneity can be represented in a hierarchical framework that consists of biogeographic provinces, biomes, biogeomorphic features, terrains, and finer scales. The Australian government is using a hierarchical approach to identify bioregions for management purposes; a key aim is to ensure that a National Representative System of Marine Protected Areas (NRSMPA) will meet the requirement of comprehensiveness, adequacy and representativeness. Important findings from this study are that the provincial structure of invertebrate megabenthos broadly aligns with the provincial structure derived earlier from the distribution of fishes, but there are differences in the distribution of individual major taxa at both provincial and megahabitat scales. Representative coverage of rarer taxa or narrowly distributed taxa might not be feasible at the same time as ensuring main fauna groups are adequately represented. The hierarchical scales of heterogeneity of the megabenthos in this area, the differences between taxa, and the high proportion of apparently rare species make it clear that it will be as important to manage the area outside the NRSMPA as to manage the NRSMPA itself. Management will be required at different scales that correspond to the multi-scale spatial heterogeneity of continental margin fauna.

Problem

Species diversity in deep-sea benthic fauna exists at many spatial scales over seabed landscapes, shaped by a variety of processes acting over contemporary and evolutionary time scales (Levin *et al.* 2001; Snelgrove & Smith 2002). Influential processes linked to sediment characteristics, nutrient input and productivity, dissolved oxygen and hydrodynamics, vary at regional scales (100–1000s km²) (Levin *et al.* 2001) and at smaller scales where connected with, or modified by, habitat features or closed systems (Schaff *et al.* 1992; Hillebrand 2004; Schlacher *et al.* 2007).

Underlying the biodiversity patterns detected at regional and smaller scales are zonal changes of species abundance and richness with depth (Gage & Tyler 1992; Carney 2005), and a gradient of richness usually negatively correlated with latitude, but which varies with organism type and size, and also between regions (Zezina 1997; Hillebrand 2004). Such patterns are well studied in terrestrial and nearshore environments, but are more enigmatic in the deep sea (Poore & Wilson 1993; Rex *et al.* 1997, 2005). Modern ecological patterns have their origins in the geological history of the oceans and their surrounding continents (Briggs 1987; McGowran *et al.* 2000; Poore & O'Hara 2007), which provide the framework on which contemporary processes act. Improved understanding of the linkage between pattern and process comes from discovering how contemporary fauna and processes are geographically distributed, especially over a wide latitudinal range. But while this is being assisted by our greater capacity to gather biological and physical (habitat) data from the deep sea, ecological explanations for patterns of diversity in deep-sea fauna across diverse taxa from the same sites in a region are lacking (Haedrich *et al.* 2008).

Knowledge of Australia's deep benthic biodiversity is relatively poor, although its continental margin is massive: continental slope makes up about 45% of the 8.9 million km² of Australia's EEZ (Heap & Harris 2008). The varying form of the slope at a coarse spatial scale of 1000s km² is attributed to a complex underlying geology, with sedimentation having relatively little influence, and continental rifting on all but the northern margin (Heap & Harris 2008). Only relatively small areas of slope are mapped at high resolution, but this is changing rapidly with the routine use of multibeam sonar (MBS) and underwater photography during surveys (Kloser *et al.* 2007). Australia has committed to protecting the marine environment, including establishing a National Representative System of Marine Protected Areas (NRSMPA) by 2012. Its marine bioregionalisation, used to establish this system, is relying on a biogeography based largely on

knowledge of intertidal and subtidal species, and less so on shelf species (Poore & O'Hara 2007). The biota broadly comprises overlapping temperate (southern) and tropical (northern) components, whose origins can be traced back into geological history, with gradients across the extensive southern coast (O'Hara & Poore 2000). Within these regional-scale patterns, effective conservation planning requires an understanding of the sub-structure of habitat and process heterogeneity, and their influences on biodiversity. Additional knowledge of the deep shelf and upper/mid-slope (~200–1500 m) is of particular importance because in these offshore waters, targeted human impacts coincide with the highest biodiversity of megabenthic epifauna (Williams *et al.* 2009).

Planning for conservation of biodiversity in Australian waters cannot credibly extend to the benthic invertebrate megafauna on the continental margin without a systematic description of its diversity and habitat at different scales. In this paper we report on the megabenthos diversity on Australia's extensive south-western margin based on a survey between ~18° S and 35° S at depths of ~100–1100 m. Following Greene *et al.* (1997, 2007), biological and habitat scales are termed 'regional' (scales of >1000s km), 'provincial' (~100–1000 km), 'megahabitat' (~km–10s km) and 'mesohabitat' (~10s m–1 km). Specifically we aimed to (i) determine the patterns of biodiversity for several major taxa of megabenthos, (ii) determine the influences of physical environmental covariates on the distribution of megabenthos species richness and assemblage structure, and (iii) link these explicitly to spatial scales.

Material and Methods

Field survey

The epibenthic invertebrate megafauna of the south-western continental margin of Australia was sampled from the FRV *Southern Surveyor* in 2005 (survey SS 10-2005). The survey was designed to sample at four nested hierarchical spatial scales that would represent habitat heterogeneity. At the coarsest scales these habitats were (i) biogeographic provinces (Commonwealth of Australia, 2005), and then (ii) biomes (depth-related zones), defined previously by indices generated from the distributional ranges of benthic fishes (Last *et al.* 2005). The next levels were based on physical attributes of the seabed existing at megahabitat scales of 100s of km (*sensu* Greene *et al.* 2007). These were (iii) geomorphic features defined primarily by seafloor topography (Heap & Harris 2008) (canyons, seamounts and sediment terraces), within which (iv) terrains (Kloser *et al.* 2007) were formed predominantly by either sediment (soft) or rocky (hard)

substrata. Sites for biological sampling were selected on the basis of topographic data gathered using multibeam sonar (MBS) during a companion survey in 2005.

Provincial-scale coverage was achieved by locating 19 sites at 1° intervals: latitudinal from Barrow Island ($\sim 21^\circ$ S, 116° E) to Point D'Entrecasteaux and then, following the change in direction of the coastline, longitudinal to Bald Island ($\sim 35^\circ$ S, 119° E) (Fig. 1). The intervals were set at not exactly 1° to avoid areas that commercial fishery logbook data showed had been bottom-trawled. The depth horizons sampled at each 1° represented the biomes of the outer continental shelf (~ 100 m depth) and the upper continental slope (~ 400 m depth); additional depths (200, 700 and 1000 m) were sampled at

some sites. The fine-scale placement of sample sites was at the closest point to a pre-determined $1^\circ \times$ depth location where sediment substrate was confirmed by MBS mapping. Geomorphic features and hard seabed terrains were sampled opportunistically: selected features were targeted, whereas hard terrains were sampled wherever they existed at, or adjacent to, the $1^\circ \times$ depth sites or formed parts of features. Overall, 118 successful samples were taken from the 19 sites (Fig. 1).

An epibenthic beam trawl based on the French IRD design (<http://www.cmar.csiro.au/research/seamounts/epibenthic.htm>) with a mouth width of 4 m was used to collect samples on sediment terrains with depth-parallel tows of 20 min duration. A robust epibenthic sled (Lewis

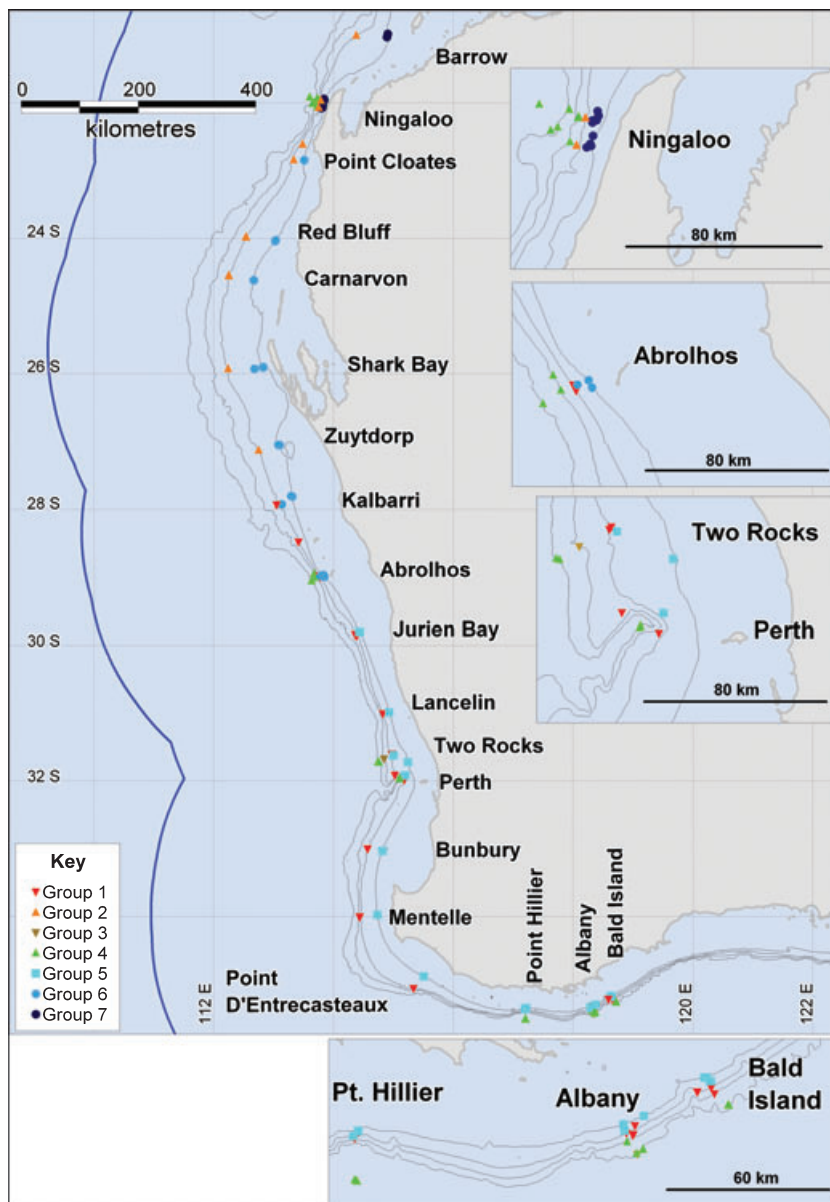


Fig. 1. Locations of 118 epibenthic sled samples of benthic invertebrate megafauna from 19 sites on Australia's south-western continental margin. Symbols are consistent with groups identified by Linktree analysis (Figs 3 and 4).

1999) with a mouth width of 1.2 m was used on the hard terrains and steep areas of geomorphic features where tow direction and duration were dictated by the roughness and extent of rocky bottom. Both samplers had large cod-ends made of 25-mm stretched-mesh net. Tow distances along the seabed were measured using an Ultra Short Baseline (USBL) beacon to determine the duration of bottom contact, and dynamic GIS mapping (MapInfo LinkLite) to plot the tow track. Catch data were standardised for the swept area of individual tows.

Biological samples

Samples of megabenthos were sorted by a team of taxonomists to the lowest resolution possible at sea, and each taxon was weighed and counted. Examples of each of these interim 'operational taxonomic units' (OTUs) were photographed, and the catch preserved and catalogued after each sample to ensure consistency in the shipboard identifications. All material was preserved and retained, and distributed to museum experts for taxonomic refinement. Seven major taxa [Demospongiae, Decapoda, corals (Octocorallia and Antipatharia), Mollusca, Echinodermata, Ascidiacea and Pycnogonida] were selected for this study following considerable taxonomic refinement and more accurate identifications in the lab (participating taxonomists listed in Acknowledgements). A checklist of all

species is provided by McEnnulty *et al.* (in prep.); commentaries on some registered sub-collections were provided by Poore *et al.* (2008) and Kott (2008); data have been provided to the Census of Marine Life databases through OBIS and the Continental Margins Program, COMARGE. In the 118 samples used for this analysis, 4431 records were derived from 1979 species in 346 families (Table 1).

Physical data

The physical covariates considered to be relatively stable over time (*e.g.* sediment properties and acoustically sensed bottom types) were estimated for the mid-points of sled tows. Sediment data were interpolated and gridded to 1-km cells by Geoscience Australia; these provided four covariates (grain size as percentage of mud, sand and gravel, and percentage of carbonate). Multibeam sonar backscatter data were used to quantify the relative hardness of the substrate and provided two covariates. These were a weighted average and standard deviation of backscatter, estimated using a Gaussian kernel along each sample tow. Backscatter was corrected for seabed slope and water column absorption, with the local incidence-angle dependency removed by a long-term average and referenced to the average 40° incidence-angle backscatter (Kloser *et al.* 2007). This processing method minimises

Table 1. Summary of composition and distribution of benthic invertebrate megafauna from the south-western Australian continental margin showing the number of families, species and unnamed species in taxa analysed; their distribution over sample groups formed from ordination analysis (Figs 3 and 4); and their relative contributions to within group similarity based on SIMPER analysis.

	Families (n)	Species (n)	Unnamed and new species (%)	Linktree group						
				1	2	3	4	5	6	7
(a) Species richness of major taxa										
Demosponges	47	361	95	19	0	1	2	265	144	58
Corals	28	153	77	27	7	7	15	33	59	39
Molluscs	107	489	67	121	81	2	80	77	132	110
Echinoderms	71	358	39	87	48	22	82	61	119	75
Decapods	74	523	33	92	100	9	94	85	185	159
Ascidians	14	81	33	9	3	0	1	56	30	1
(Pycnogonids)	5	14	43	0	0	0	2	7	6	1
All taxa	346	1979	–	355	239	41	276	584	675	443
Bray-Curtis similarity (within-group average)				8.3	6.57	21.8	3.92	4.86	5.1	5.09
(b) % contribution to within group similarity										
Demosponges				0.03	0	0	0	30.8	5	9.08
Corals				0.7	1.38	20.1	0.97	4.61	1	3.41
Molluscs				5.98	8.5	0	12.2	6.46	8.5	8.47
Echinoderms				59.9	13	78.4	57.1	21.6	13	8.37
Decapods				33.3	77.3	1.53	29.7	32.5	71	70.5
Ascidians				0.14	0	0	0	3.95	1.6	0
(Pycnogonids)				0	0	0	0	0.06	0.1	0.18

many of the errors inherent in uncalibrated backscatter data while preserving the highest spatial-scale information. Covariates considered to vary on annual, seasonal or finer time scales (e.g. oceanographic properties) were interpolated from data accumulated over an extended period of time. Interpolated data provide information on the physical environment that the biota is exposed to over lifetime, rather than the environment at the time that the sample was taken. Oceanographic data were mostly from the CSIRO Atlas of Regional Seas, an interpolated oceanographic data set (CARS 2006, <http://www.marine.csiro.au/~dunn/cars2006/>); these provided nine covariates as depth-specific means, standard deviations and ranges of temperature, salinity and oxygen concentration. Depth and latitude were also used in the covariate dataset.

Analytical methods

The multispecies similarities of the 118 samples were determined with a Bray–Curtis similarity measure of untransformed species abundance (count) data standardised by sampling area. The samples were grouped using environmental covariates in a regression tree. For this analysis we used the Linktree routine in the PRIMER v6 (Clarke & Gorley 2006) [a modification of the multivariate regression trees described by De'ath (2002)], which sequentially divides samples into dichotomous groups determined by grouping structure within the biological similarity matrix and the power of covariates to explain the splitting points. These were identified using the SIMPROF routine in PRIMER v6 (Clarke & Gorley 2006). Non-metric multidimensional scaling ordinations (nMDS) were used to graphically represent the patterns in the species composition between samples. The taxa typifying the groups were identified by the SIMPER routine (Clarke 1993). All 1979 species in the 118 samples were included in the analysis.

The species richness of each major taxon is simply the number of species per sample. Its relationship to the physical covariates was analysed using a Generalised Linear Model (GLM) with a negative binomial distribution and a log link function. To calculate standardised species richness per sample, we used an offset in the GLM of log (area sampled) to standardise all samples to a common unit of area in the analysis. Models were selected using a combination of forward and backward selection based on the Akaike information criterion (Akaike 1974). The model fit was diagnosed using model residuals. We examined the relationship between each covariate and richness separately by examining the marginal relationships, *i.e.* holding all other covariates at their mean values. This allows the examination of effects due to a single covariate in isolation.

Results

Composition and diversity of megabenthos

Four of the seven taxonomic groups contributed the bulk of the 1979 species identified; Decapoda were represented by 523 species, Mollusca by 489 species; and Demospongia and Echinodermata each by about 360 species (Table 1a). These figures underestimate total invertebrate megafaunal richness because several other major taxa were excluded from this study (e.g. Bryozoa, Hydrozoa). The selected taxa had a high proportion of unnamed or new species (57% overall; range 33–95%) (Table 1). The fauna was characterised by high beta-diversity and high apparent rarity: over 50% of all species were caught in a single sample, of which more than two-thirds (706 species) were represented by single individuals. Only 14 species caught in a single sample were represented by 20 or more individuals. Species caught in two samples made up another 19% (383 species), while 15 species were found in 12 or more samples (*i.e.* >10% of all 118 samples).

Mapping and scales of covariates

The correlation between temperature and depth is maintained over a wide latitudinal range, while the correlation between mean oxygen and depth varies with latitude (Fig. 2A,B). Bottom types are heterogeneous at a variety of sub-regional scales, with distributions of hard substrate varying with depth and latitude over regional scales, geomorphic features at megahabitat scale, and patchiness at local or mesohabitat scale (Fig. 2C). The high correlation between many of the physical covariates calls for caution in inferring causality from these data.

Megabenthos distribution in relation to habitat heterogeneity

The regression tree (Linktree) analysis of the Bray–Curtis similarity matrix split the 118 biological samples with environmental covariates into 35 end-node groups: 21 groups of multiple samples without significant group structure (SIMPROF π : $P > 0.1$) and 14 singletons (Fig. 3). For the broad-scale interpretation we concentrated on the main groups formed by the first three splits along each branch of the tree (Table 2), which created seven sample groups and two single samples (Fig. 3). These splits clearly correspond to the structure of the multispecies similarity data represented in two-dimensional ordination space (Fig. 4A).

Covariate values driving the first three splits are detailed in Table 2. The first split differentiated groups 1–4 from groups 5–7 on mean temperature, with a singleton sample (the deepest at 1588 m) split on depth and temperature. The greatest difference in overall species compo-

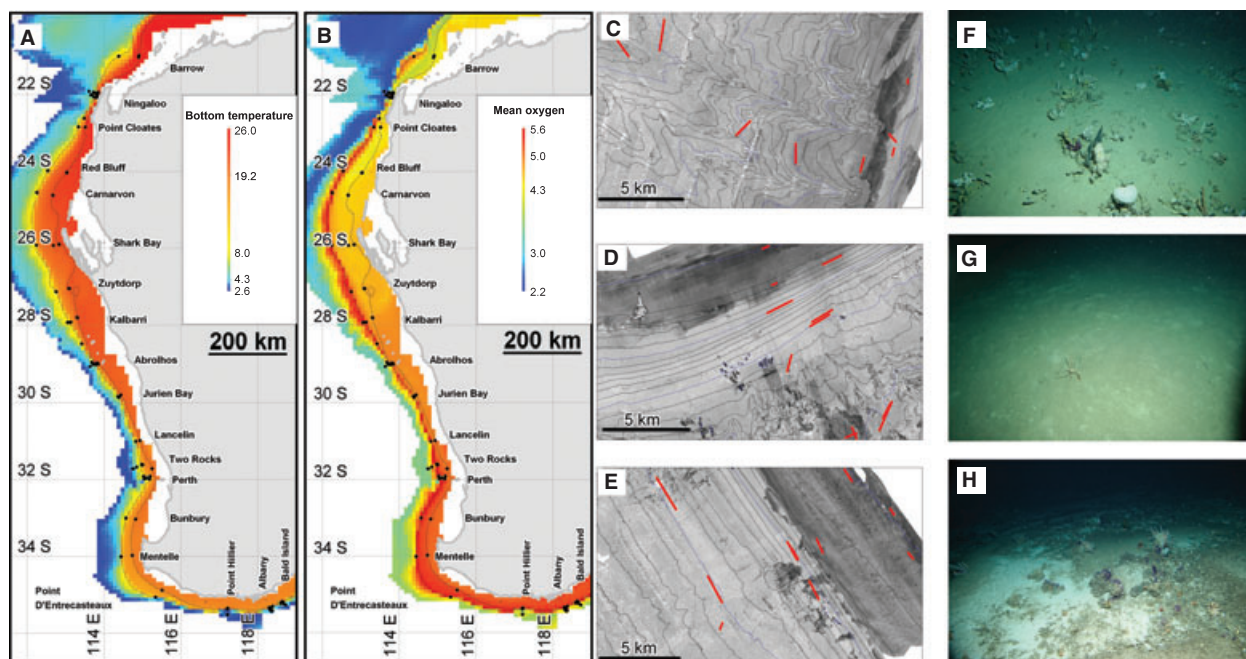


Fig. 2. Mapping of physical environmental (habitat) covariates of invertebrate megafauna on Australia's south-western continental margin: (A) regional-scale temperature at seabed; (B) regional-scale mean oxygen concentration at seabed; (C–E) megahabitat-scale examples of seabed type from multibeam sonar (darker shading = harder/rougher bottom; red lines show sample sites). (F–H) Examples of megabenthic communities at scales below mesohabitat: (F) dense patches of sponges and colonial ascidians hard subcrop with veneer of muddy sediments at 254 m depth off Kalbarri; (G) spider crab on bioturbated muddy sediments at 461 m depth off Perth; (H) patches of dead and live coral debris (*Solenosmilia* sp.) and muddy sediments with octocorals, orange solitary corals and glass sponges at 998 m depth off Albany.

sition was therefore between samples taken from the warmer deep continental shelf (right branch of the tree) and the colder continental slope (left branch) (see Fig. 2A). On the slope branch, mean temperature and mean oxygen split groups 1 and 2 from groups 3 and 4, differentiating upper slope from mid-slope samples. The second singleton, the second deepest sample (1259 m depth) and from near the northern limit of sampling, was split from groups 1 and 2 by depth and latitude. Group 1 was split from group 2 by latitude, south and north of Kalbarri, respectively. Variance in backscatter split the mid-slope groups 3 and 4 with three samples of high backscatter variance (group 3), one off Two Rocks and two close to each other off Albany. On the right branch of the tree containing deep continental shelf samples, latitude split group 5 from 6 and 7, south and north of Jurien Bay, respectively (Fig. 1). Group 5 was not split further, as the two subsequent splits created only singleton samples (Fig. 3). Mean oxygen and latitude split group 6 from group 7 at Point Cloates, with samples north of this point characterised by low oxygen.

The consistency of between-sample similarities was assessed by comparing the similarity matrices produced by each major taxon separately; samples containing no species from a taxon and outliers were removed from the

analyses. The comparison showed that the multitaxa groups generated by the Linktree analysis were not always maintained by the individual taxa (Fig. 4), especially those taxa that made little contribution to within-group similarities in the earlier analysis (Table 1). Decapods, molluscs and echinoderms were relatively rich, most widely distributed over samples and sample groups, and preserved the 'all-taxa' pattern most closely. Deep shelf was consistently differentiated from slope, whereas the group of mid-slope soft bottom samples (group 4) and group of southern deep shelf samples (group 5) were most stable; upper slope samples (groups 1 and 2) and northern deep shelf samples were less clearly differentiated. Corals were relatively species-poor and not present in >30% of samples, but were represented in each group. They differentiated deep shelf from slope, but other patterns were not evident. All-taxa patterns were not preserved by the remaining major taxon (sponges) or a minor taxon (ascidians), both being relatively species-poor, absent from >60% of samples, and poorly represented in slope groups 1–4.

Species richness

Patterns of standardised species richness varied in a complex and non-linear manner with physical covariates

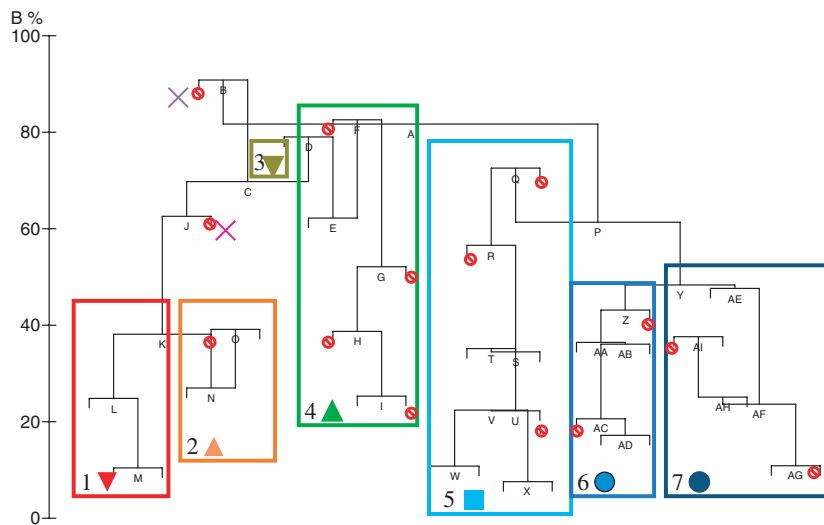


Fig. 3. The arrangement of sample groupings derived from regression tree (Linktree) analysis of 1979 benthic invertebrate megafaunal species in 118 epibenthic sled samples from Australia's south-western continental margin. Red symbols indicate single-sample end-nodes; other symbols match those used in Figs 1 and 4 to show, respectively, the geographical locations of samples and sample similarities in ordination space.

Table 2. Physical environmental co-variables with greatest correlation to multispecies patterns in Linktree analysis (Fig. 3) of Bray-Curtis similarity matrix of 1979 dominant invertebrate megafaunal species from Australia's south-western continental margin.

Group	Split 1	Split 2	Split 3	Geography
1	<14.4°C	>7.11°C & >4.78 O ₂	>27.9°S	(see below)
2			<27.9°S	
3		<6.82°C & <4.75 O ₂	>-31.9 dB (SD)	
4			<-35.1 dB (SD)	
5	>14.4°C	>29.8°S	-	
6		<29.0°S	>22.8°S & >4.44 O ₂	
7			<22.1°S & <4.29 O ₂	
1	Cold	Warm & high O ₂	South	Upper slope; south of Kalbarri
2	Cold	Warm & high O ₂	North	Upper slope; north of Kalbarri
3	Cold	Cold & low O ₂	Hard seabed	Mid-slope
4	Cold	Cold & low O ₂	Soft seabed	Mid-slope
5	Warm	South	-	Deep shelf; south of Jurien Bay
6	Warm	North	South & high O ₂	Deep shelf; Jurien Bay to Point Cloates
7	Warm	North	North & low O ₂	Deep shelf; Point Cloates to Barrow Island

(Appendix and Fig. 5). Each major taxon responded in different ways to different covariates, with no single consistent pattern and no single covariate highly predictive of richness. However, the influences on species richness of individual covariates (examined with all other covariates held at their mean values) showed strong relationships with some major taxa on several scales (Fig. 5). Taxa that did not vary with a particular covariate are shown as a straight line with the intercept equal to the mean richness value for that taxon. The marginal relationships show the effect of varying just a single covariate and are smooth functions over the range of covariates.

Most major taxa showed relationships with mean backscatter, which varied on relatively small spatial scales

(Fig. 5A). The relationships of molluscs, echinoderms and sponges were strong, with richness increasing with increasing hardness (*i.e.* backscatter >-30). At intermediate levels of backscatter, decapods had maximum richness, and corals minimum richness. Ascidiarians showed a weak relationship. Note, however, that modelled relationships are less reliable towards both the maximum and minimum covariate values due to low sample numbers.

Major taxa responded differently to covariates that varied on relatively large spatial scales. The richness of echinoderms and corals increased with increasing mean temperature (Fig. 5B), whereas sponge richness increased with increasing variation in temperature, and coral richness increased with low variation in temperature (Fig. 5C). Covariates that varied at intermediate scales also influenced



Fig. 4. Ordination (nMDS) plot of 118 epibenthic sled samples from Australia's south-western continental margin based on a Bray–Curtis similarity matrix of 1979 dominant benthic invertebrate megafaunal species. Symbols show groupings identified by Linktree analysis in Fig. 3.

richness, e.g. coral richness decreased markedly with an increased percentage of mud (Fig. 5D). Further, there were interactions between the responses at large and small scales, e.g. decapod richness was correlated with the interaction between backscatter and mean oxygen (see Appendix).

Discussion

Characteristics of megabenthos diversity on the continental margin

This collection of epibenthic megafauna reveals that Australia's south-western continental margin ($\sim 18^\circ$ S– 35° S) supports a previously unknown high species richness and novelty in several invertebrate taxa (Table 1). For example, 76 species were added to the Decapoda covered

in Poore's (2004) guide to the fauna of southern Australia – a 9.4% increase. This reflects the fact that the region has been rarely explored. The identifiable species had been previously recorded from shallower shelf depths, the Southern Australian coast, or from the Indo–West Pacific.

Many species (60–70% of the total) were rare, being found in just one or two of the 118 samples taken. These fractions are greater than those of some other megafaunal studies in Australian waters, e.g. 30% of species were found only once in 1340 samples taken in an extensive survey on the continental shelf off Queensland (Pitcher *et al.* 2007) and 56% of fishes on the western slope were taken in one or two trawls (Williams *et al.* 2001). Our estimate approaches that found in other poorly explored environments, e.g. 76% of sponge species in deep south-

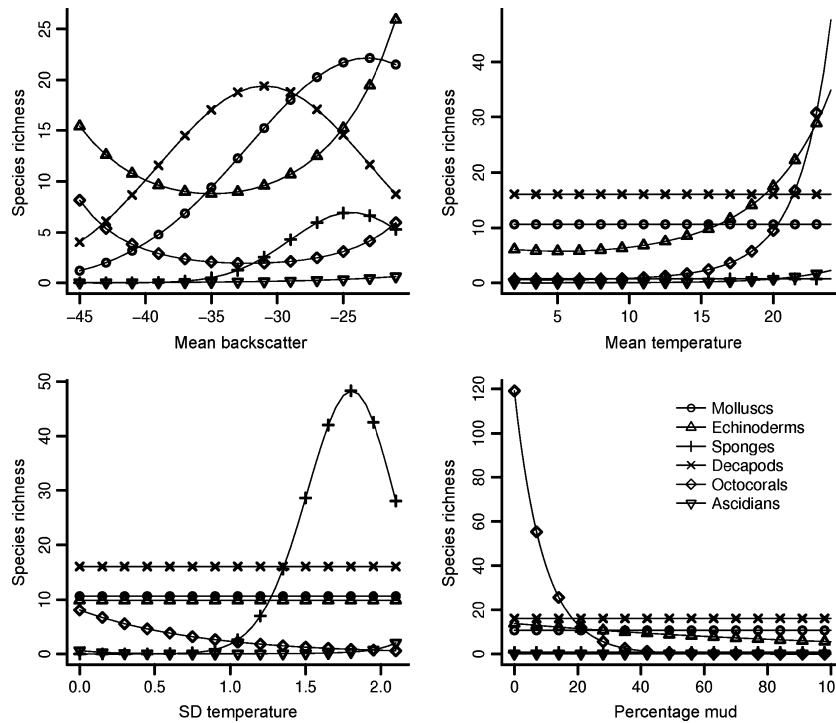


Fig. 5. The influence of individual physical environmental covariates on invertebrate megafaunal species richness on Australia's south-western continental margin using a Generalised Linear Model approach to hold all other covariates at their mean values.

eastern canyons were found at single sites (Schlacher *et al.* 2007). Apparent rarity is a common finding in megafaunal studies, but most studies (this one included) do not include the replicate sampling that would be necessary to distinguish rarity from sampling efficiency or patchiness.

Scales and roles of habitat heterogeneity for biodiversity distribution

At the regional scale of the Australian south-western margin (a survey region of some 1600 km linear distance), the pattern of distribution of epibenthic megafaunal communities was best explained in the analysis by temperature and oxygen, which vary on large spatial scales. Latitude was also a high-level explanatory variable, indicating the influence of some other correlated, but unknown, factor(s). Other covariates, notably seabed type, were also important explanatory variables for community patterns at smaller megahabitat scales (10–100s of km). Among the identified important covariates, temperature and oxygen exist as vertical and horizontal gradients at the regional scale of habitat, and have strong relationships with depth and latitude (*e.g.* Fig. 2).

The greater explanatory power of physical covariates other than depth and latitude provides greater insights to the processes driving megafaunal distributions. However, the nature of the analytical methods applied here means that we cannot attribute causal relationships to any of the individual covariates we used, even those with large

explanatory power. Key mechanistic drivers may be missing from the analysis; they include those related to pressure and food availability (Carney 2005) and, in some locations, pollution (Haedrich *et al.* 2008). Most of the covariates are correlated, as the physical processes driving them are identical. However, their explanatory power varies: some are more closely linked to the scales at which megafauna vary. For example, while depth and temperature are correlated, temperature varies along the shelf independently of depth. Our goal was not to attribute causation, but to identify scales of variation and habitat heterogeneity that rely on variation in biological data and appropriate physical covariates.

Many of the covariates used here were interpolated from observations made over significant periods of time, years or longer. Due to this and the distribution of samples in space and time, we cannot expect that there would be much difference between adjacent sites. Possibly, this reduced the power of covariates to explain differences between samples, especially at smaller scales. However, megafauna will not respond to the instantaneous values of the covariates, meaning that coincident point estimates of covariates at the time of sampling are unlikely to be informative at small scales. For example, the oxygen concentration at any one time would have little impact on the long-term patterns that can be observed; long-term averages and a measure of variability, such as standard deviation, should be used to compare with faunal distributions. Neither interpolation nor coincident measure-

ments are likely to detect extreme events that are rare and outside the range expected from the interpolated data. This may include some aspects of seasonality where a sporadic annual or decadal event affects the survival or recruitment of fauna.

Isolating the independent influences of individual covariates on species richness is useful to disentangle cross-correlation of covariates, and examine the influences across taxa. Even at the taxonomic resolution of major taxon, seabed type (as measured by the mean and standard deviation of multibeam backscatter) showed strong and intuitive relationships with some major taxa. Thus, higher diversity on hard bottom (higher backscatter) was seen in sponges (sessile species, most of which require stable seabed for anchorage), and molluscs and echinoderms (including many species associated with consolidated and structured bottom types) (Fig. 5A). Richness of Decapoda, the highest of any major taxon, was greatest at intermediate scales of bottom hardness – perhaps indicating that these bottoms comprise a mixture of rocky and sedimentary substrates at mesohabitat or smaller scales (m to km) that appeals to a wide range of species. The Decapoda taken in this survey included diverse families with diverse ecological preferences, ranging from cryptic species living under rocks to species living on exposed, soft-sediment plains.

Covariates that most influenced benthic megafaunal patterns at a regional scale on the Australian south-western margin reflect ocean circulation and water mass structure. The shelf-edge to ~250–300 m depth is influenced by the Leeuwin Current (Smith *et al.* 1991; Ridgway & Condie 2004; Waite *et al.* 2007) which brings warmer, oxygen-poor tropical waters southwards; these waters cool gradually with increasing latitude as they mix with colder waters. The underlying slope is influenced by the northward-flowing, colder, oxygen-rich Leeuwin undercurrent in ~200–400 m depths (Waite *et al.* 2007), with mode and Antarctic Intermediate Water below 400 m. Thus, transitions in temperature which appear to drive the separation of continental shelf communities from those of the continental slope, with mean seabed oxygen concentration then influencing community structure on both shelf and slope, are properties of the water masses that bathe the entire south-west margin. Oxygen is consistently high at the shelf edge, but on the shelf there is a shift in oxygen concentration in mid-latitudes (~30–32° S), with concentration increasing with increasing latitude. In contrast, oxygen concentrations on the slope decrease as a function of depth, but apparently not latitude, as they are lower in the north. This indicates that the environmental covariates of community structure linked to ocean currents are interacting in different ways in different places.

Seabed types (hard and soft terrains) are highly variable in spatial scale. 'Hard' (semi-consolidated or rocky) seabed terrains range from extensive, elongate, depth-parallel rocky banks formed by paleo-coastlines and massive plains of shelf-edge coarse carbonate sediments, to scattered patches of rocky outcrop and sub-crop (e.g. Fig. 2C–E, respectively). Large contiguous areas of 'hard' terrain may exist at megahabitat scales or larger (~10–100 km), while patches may exist at only mesohabitat scale (~10s m–1 km). Despite their distributions and areal extents being only partly mapped on the Australian south-western margin, their collective areas appear to vary when viewed at the provincial or regional scale. Thus, emergent paleo-coastlines were most evident in the north (Ningaloo) and south (~>31° S), large rocky banks only in the central survey area (Abrolhos), and large areas of coarse sediments most prevalent in the south (Point Hillier to Bald Island). Local-scale aggregations of hard seabed also co-occurred with canyons (Kalbarri, Two Rocks and Perth), and a small pinnacle feature (Albany). These distributions suggest there is considerable regional-scale heterogeneity of habitats defined by sediment properties (Fig. 2F–H) that determine basic niche requirements: consolidated attachment sites for sessile fauna, and sediment classes suited to the needs of mobile and burrowing fauna (e.g. Thouzeau *et al.* 1991; Roberts & Davis 1996; Bax *et al.* 1999, Post *et al.* 2006; Kloser *et al.* 2007). The distributions of 'hard' bottom types thus represent critical elements of habitat heterogeneity nested within the larger scales of other influential covariates.

Using habitat and biodiversity information for conservation management

We have shown that megabenthos diversity along Australia's south-western margin varies at a variety of spatial scales, and have presented hypotheses that this diversity results from physical processes also acting over a range of spatial and time scales. The diversity results, at least in part, from regional-scale historical processes mixing faunal elements of the Indo-West Pacific and temperate Australia. Mixing of these faunas has been facilitated since the later middle Eocene (38 mya) by the southward-flowing Leeuwin Current that has enabled fauna of tropical origin to enter and survive in South-western Australia and to co-exist with more temperate forms (McGowran *et al.* 1997). Large-scale properties of this current and associated water masses (temperature and oxygen) had the highest power in explaining the observed provincial-scale patterns in megabenthos communities on the south-western continental margin. Although this does not determine a causal mechanism for faunal heterogeneity, the indications are that the Leeuwin Current and

associated water masses play a key role in determining megabenthos community structure at provincial scale.

Samples distinguishing groups 3 and 4 in the Linktree analysis provided information on factors affecting megabenthos patterns at the megahabitat scale. Sites in the two groups are adjacent to one another but were split based on acoustic backscatter (Fig. 3); the taxa differing most in species richness (Table 1) had the strongest response to acoustic backscatter in the GLM analysis (Fig. 5a). Bottom hardness appears to be an important modifier of megabenthos community at the megahabitat scale, but as other physical covariates were not available at a sufficiently fine-enough scale, we have to be cautious of this interpretation.

It is clear from the information derived from the variety of scales used in this study that the scale of observation strongly influences both hypotheses and inferences. The conceptual hierarchical framework we used to capture spatial scales of habitat heterogeneity is very similar to the hierarchical approach used in the developing management of Australia's marine biodiversity. It is, we believe, essential for describing, understanding, and managing biodiversity and habitat heterogeneity – especially on continental margins.

The Australian government developed bioregional planning as a framework for managing its marine environment (Commonwealth of Australia, 2005; Heap *et al.* 2005). A key aim is to ensure that the developing National Representative System of Marine Protected Areas (NRSMPA) meets the requirement of comprehensiveness, adequacy and representativeness (the 'CAR' principles, ANZECC 1998). An important finding from our study was that the provincial structure of megabenthos in the area of study broadly aligns with the provincial structure based on fishes, which was used to delimit bioregions to meet the management requirement of comprehensiveness. Ensuring that the NRSMPA is represented in each bioregion should provide for comprehensive management of Australia's marine fauna, or at least for megabenthic invertebrate and fish fauna.

Our study has also highlighted that taxa are differentially distributed at the provincial and megahabitat scales. The distribution patterns of the relatively species-rich decapods, molluscs and echinoderms were each similar to the distribution patterns of all taxa combined. Rarer taxa either did not show the more detailed patterns (corals) or had narrower distributions (ascidians). Sponges, a relatively species-rich taxon, also had a narrow distribution and, similarly to ascidians, had few representatives on the slope. This may also be true of minor taxa not examined. Thus, achieving representative coverage of rarer taxa or taxa with narrow distributions might not be feasible at the same time as achieving adequate representation of the

major faunal groups. The narrow distribution of sponges and ascidians in particular shows the importance of adequately representing shelf-edge habitats in the NRSMPA, which despite ease of identification has been difficult to achieve to date (Williams *et al.* 2009).

The hierarchical scales of heterogeneity of the megabenthos in this area, the differences between taxa, and the high proportion of apparently rare species make it clear that it will be as important to manage the area outside the NRSMPA as to manage the NRSMPA itself. Management will be required at the different scales that correspond to the spatial heterogeneity of continental margin fauna. This will require the development of additional management instruments focused at the spatial scales and heterogeneity that marine-protected areas fail to address.

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Appendix

Model fits and estimates for GLM-based analysis of six major taxa. Values for the over-dispersion parameter (Theta) and Null and Residual deviances are shown for each major taxon.

	Estimate	SE	z value	Pr(> z)
Ascidians				
(Intercept)	1.09E+006	2.99E+005	3.642	0.000271
Mean salinity	-9.31E+004	2.55E+004	-3.655	0.000257
Latitude	-1.11E+001	6.92E+000	-1.608	0.107734
Mean backscatter	1.50E-001	4.21E-002	3.561	0.000369
Percentage gravel	2.08E+000	6.35E-001	3.281	0.001033
SD temperature	-7.23E+000	3.21E+000	-2.255	0.024107
Mean oxygen	5.66E+000	1.67E+000	3.394	0.000690
Mean salinity ^2	2.65E+003	7.23E+002	3.667	0.000245
Mean salinity ^3	-2.52E+001	6.84E+000	-3.679	0.000234
SD temp ^2	2.96E+000	1.15E+000	2.586	0.009721
Mean temperature	2.89E-001	1.41E-001	2.056	0.039790
Mean salinity:latitude	3.18E-001	1.97E-001	1.62	0.105321
Percentage gravel: mean oxygen	-5.54E-001	1.70E-001	-3.259	0.001117
Percentage gravel:SD temp	5.22E-001	1.94E-001	2.695	0.007048
Theta	4.18	2.02		
Null deviance		626.152	Df = 117	
Residual deviance		67.454	Df = 104	
Decapods				
(Intercept)	-2.27E+001	5.99E+000	-3.791	0.00015
Depth	-2.83E-003	3.06E-004	-9.23	<2e-16
Mean backscatter	-8.44E-001	2.42E-001	-3.481	0.00050
Mean backscatter ^2	-8.01E-003	3.02E-003	-2.653	0.00797
Percentage gravel	4.81E-002	1.98E-002	2.43	0.01510
Mean oxygen	2.31E+000	1.05E+000	2.214	0.02681
Mean backscatter:Mean oxygen	7.31E-002	3.04E-002	2.405	0.01615
Theta	2.70E+000	4.46E-001		
Null deviance		3.51E+002	Df = 117	
Residual deviance		1.29E+002	Df = 111	
Echinoderms				
(Intercept)	-4.9519822	3.3151176	-1.494	0.13524
Percentage mud	0.0491625	0.0176296	2.789	0.00529
Mean backscatter	0.3886292	0.2032387	1.912	0.05585
Variance in backscatter	0.1136128	0.0236634	4.801	1.58e-06
Latitude	-0.1423347	0.0323529	-4.399	1.09e-05
Mean temperature	0.0422143	0.0626903	0.673	0.50071
Mean temperature ^2	0.0051412	0.0022212	2.315	0.02064
Mean backscatter ^2	0.0055605	0.0031946	1.741	0.08176
Variance in backscatter ^2	-0.0006549	0.0003579	-1.83	0.06730
Variance in backscatter:Mean Temperature	-0.0055214	0.0010881	-5.074	3.89e-07
Percentage mud:latitude	0.002008	0.0006419	3.128	0.00176
Theta	2.746	0.501		
Null deviance		310.43	Df = 117	
Residual deviance		130.3	Df = 107	
Molluscs				
(Intercept)	-7.476566	3.628291	-2.061	0.0393
Depth	-0.001772	0.000278	-6.374	1.85e-10
Mean backscatter	-0.285383	0.227166	-1.256	0.209
Mean backscatter ^2	-0.006152	0.003512	-1.752	0.0798
Theta	1.95	0.334		
Null deviance		268.25	Df = 117	
Residual deviance		133.48	Df = 114	

Appendix Continued.

	Estimate	SE	z value	Pr(> z)
Corals				
(Intercept)	14.4696925	6.0405906	2.395	0.016602
Mean backscatter	0.6456747	0.3253068	1.985	0.047165
Mean temperature	-0.0915859	0.1520246	-0.602	0.54688
Variance in backscatter	0.5173528	0.1221367	4.236	2.28e-05
Percentage mud	-0.410376	0.0864776	-4.745	2.08e-06
Variance in backscatter.sq	-0.001061	0.0007398	-1.434	0.151528
Mean temperature.sq	0.0112161	0.0042976	2.61	0.009059
Mean backscatter.sq	0.0089105	0.0054839	1.625	0.104195
Percentage sand	-0.1027139	0.0392708	-2.616	0.008909
SD temperature	-2.9255839	1.0681973	-2.739	0.006166
Mean temperature:variance in backscatter	-0.011639	0.0030614	-3.802	0.000144
Mean temperature:percentage mud	0.0056342	0.0011848	4.755	1.98e-06
Mean backscatter:percentage mud	-0.0068137	0.0021273	-3.203	0.001360
Mean backscatter:variance in backscatter	0.0100595	0.0036527	2.754	0.005888
Variance in backscatter:SD temperature	0.0962224	0.0418704	2.298	0.021556
Theta	1.47	0.343		
Null deviance		353.97	Df = 117	
Residual deviance		111.81	Df = 103	
Demosponges				
(Intercept)	-51.671443	10.856574	-4.759	1.94e-06
SD temperature	28.320972	5.147585	5.502	3.76e-08
Mean backscatter	-1.220035	0.582862	-2.093	0.036333
Mean backscatter ^2	-0.024756	0.009592	-2.581	0.009856
SD temperature ^2	-4.156263	1.446284	-2.874	0.004056
Latitude	-0.687047	0.167069	-4.112	3.92e-05
SD temperature:latitude	0.433095	0.130667	3.314	0.000918
Theta	0.498	0.104		
Null deviance		371.767	117	
Residual deviance		79.918	111	