Australia’s deep-water reserve network: implications of false homogeneity for classifying abiotic surrogates of biodiversity

Alan Williams, Nicholas J. Bax, Rudy J. Kloser, Franziska Althaus, Bruce Barker, and Gordon Keith

Australia’s southeast network of deep-water marine reserves, declared in July 2007, was designed using a hierarchy that represented the distribution of marine biodiversity as a nested set of bioregions. In this hierarchy, geomorphic units, individual or aggregations of seabed geomorphic features, are the finest scale used in the design process. We evaluated the interaction between two hierarchical levels (depth and geomorphic features), using video survey data on seamounts and submarine canyons. False within-class homogeneity indicated that depth, size, complexity, configuration, and anthropogenic impact need to be added as modifiers to allow geomorphic features to act as surrogates for biodiversity distribution. A consequence of using unmodified geomorphic surrogates, and of not correctly nesting geomorphic features within depth, is the diminished recognition of the importance and comparative rarity of megafaunal biodiversity of the continental margin (<1500-m depths). We call this area the zone of importance, because it is where targeted marine impacts coincide with the greatest megafaunal biodiversity. Refining the geomorphic classification is desirable for future biodiversity characterization, but an alternative approach is to define patterns in biodiversity and abiotic variables jointly, and to utilize finer scale information and provide a classification that preserves the maximum information of both datasets.

Keywords: Australia, benthic habitats, biodiversity surrogates, classification, deep-sea environments, Marine Protected Areas, surrogates.

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Introduction

Australia’s long-term commitment to protecting the environment through the use of Marine Protected Areas (MPAs) began in 1975, with the declaration of the Great Barrier Reef Marine Park. In the 1980s, a number of small MPAs was created, but it was not until 1991 that a commitment was made to develop a National Representative System of Marine Protected Areas (NRSMPA). This commitment was renewed in 1993, with the ratification of the 1992 Convention on Biodiversity and, at the 2002 World Summit on Sustainable Development, Australia (and many other nations) committed to completing an NRSMPA by 2012. The Australian government linked the development of its NRSMPA with a national plan for marine bioregionalization that is currently being developed under its Oceans Policy (DEW, 1998a, b). The first MPA network under the NRSMPA was formally declared in July 2007.

Australia’s marine area (16 million km²) includes the third largest exclusive economic zone (EEZ) in the world (11 million km²). Its highly diverse flora and fauna include a southern component in which endemism is very high (Poore and O’Hara, 2007), and a northern component containing many elements from the ultra-diverse, tropical Indo-West Pacific biodiversity hotspot. Much of this rich and complex marine biodiversity remains poorly sampled. For example, surveys of the continental shelf and slope typically find that 30–50% of better-known groups, such as the decapods, are new to science (Poore et al., 2008), with many of the remaining species previously unreported from Australian waters. Developing an NRSMPA that is comprehensive, adequate, and representative is therefore a challenging prospect, especially by the 2012 target. Australia is taking a hierarchical approach to managing its marine biodiversity by defining a nested set of bioregions for developing the NRSMPA. Bioregions have been grouped in five large marine planning regions (Figure 1, inset), and a network of MPAs is being developed for each planning region.

At the highest level in the hierarchy of bioregions, 15 large provinces separated by ten transition zones (biotones) are defined by oceanographic information and discontinuities in the distributions of fish, the marine group for which the most synoptic species-level taxonomic information is available. Levels 2 and 3 of the hierarchy are determined primarily by the contemporary environment. Depth provides the structure for the second level, biomes, because the association of depth with patterns in the distribution of invertebrates and fish is generally well described for the Australian deep-marine fauna (Ponder et al., 2002; Last et al., 2005). The third level of this pseudo-spatial hierarchy is defined by geomorphic units, consisting of individual or aggregations of physical seabed geomorphic features, defined at a variety of spatial scales with a geological classification of historical bathymetric and geological datasets (Harris et al., 2005).

Our aim in this paper is to investigate the degree to which geomorphic features act as surrogates for benthic megafaunal biodiversity, using video survey data, some of which were not available when the design process occurred. Because geomorphic...
features had a strong influence on locating reserves in the southeast planning region, and will be similarly important for each of the other four Australian planning regions, they would ideally be proven surrogates for patterns in marine biodiversity and be biogeomorphic features. In practice, and at least partly because of the political imperative to develop an NRSMPA by 2012, geomorphic features remain unvalidated surrogates for biodiversity distribution. However, our ability to evaluate and refine feature classifications is advancing rapidly. Multibeam acoustic mapping technology provides detailed location, shape, and structure at the scale of whole geomorphic features (hundreds of square kilometres or "megahabitat" scale, sensu Greene et al., 1999), including information on substratum types that is relevant to the association of fauna with different seabed types (Kloser et al., 2007). Photographic technology (Shortis et al., in press), in combination with physical sampling, provides the matching information on composition and distribution of the biodiversity at finer scales (metres to hundreds of metres, meso- and macrohabitat scales, sensu Greene et al., 1999).

We concentrate on two influential geomorphic features, seamounts and submarine canyons, and determine whether or not they provided an accurate representation of biodiversity distribution for Australia’s southeast reserve network. First, we review their dependence on biomes (depth-related faunal distributions), the next higher level in the classification. Second, and following Stevens and Connolly (2004), we investigate the nature and prevalence of “false homogeneity”, failing to differentiate similar features that support different biological distributions. Our findings demonstrate that the design process placed insufficient emphasis on the hierarchical relationship between biomes and geomorphic features, and failed to identify some areas of differing biodiversity. We discuss the benefits that will result from refining the classification of geomorphic features, and alternative approaches using abiotic surrogates for regional- or national-scale reserve network design.

The southeast reserve network: context

Australia’s network of Commonwealth Marine Reserves (CMRs) is being established in ocean areas under Commonwealth jurisdiction. The southeast network of 13 CMRs, declared in July 2007, covers 226 458 km² of the 1 156 000 km² planning region and is the first temperate “deep-sea” network of marine reserves in the world (Turnbull, 2007; Figure 1).

Depth-related environmental processes produce the strongest gradient structuring marine benthic biological communities (Ponder et al., 2002; Last et al., 2005). In Australia’s southeast region, and in all other planning regions, the continental margin (shelf, upper, and mid-slope in depths of ~50–1500 m) provides a variety of habitats and supports a high diversity of megafauna, including benthic fish, large invertebrates, seabirds, and marine mammals. Much of this megafauna is restricted to the continental margin, which is narrow around much of Australia, relative to the width of the EEZ. The most significant direct threat to megafauna and the ecosystems of which they are part is commercial fishing, which is widespread in the relatively narrow depth range of ~50–1300 m (Larcombe et al., 2002). Other potential direct threats are less important: areas of active or prospective oil and gas extraction are excluded from CMRs; there is no seabed mining for polymetallic nodules, manganese crusts, massive sulphides, or methane hydrates, because prospects appear low (Murton et al., 2001); regulations prevent impacts from shipping (merchant and leisure) by controlling offshore dumping of terrestrial waste (ISA, 2001); aquaculture and tourism-related activities and recreational fishing are largely confined to waters inshore of Commonwealth jurisdiction (three nautical miles; Larcombe et al., 2002). Ocean acidification (Roberts et al., 2006) and

Figure 1. Australia’s southeast planning region showing the CMR network with the zone of importance (where the highest biodiversity conservation values and the greatest threats overlap) shaded. Also shown, the Australian EZ boundary at 200 nautical miles, and the shelf edge 200-m isobath. Inset: Australia’s five marine planning regions; the southeast region (excluding the Subantarctic Macquarie Island) is shaded.
climate warming are indirect threats with unpredictable magnitude and are not confined to one depth. In this paper, the area of continental margin, 1500 m was defined as the zone of importance. This is where the highest biodiversity conservation values and the greatest threats overlap. It is the area likely to benefit the most from conservation planning and affect the largest number of current (direct) marine users.

Geophysical classification

In all, 21 feature types, reduced from the 53 types endorsed by the International Hydrographic Organisation (IHO, 2001), were identified and mapped for the southeast region (Figure 2; and see summary in Harris, 2007). Large individual geomorphic features and aggregations of features were used to define geomorphic units. Geomorphic units served to identify broad areas of interest within the southeast region, within which marine reserves were proposed. Individual geomorphic features were used to address the design criteria (Anon., 2003), e.g. "select at least two canyons next to each other and include intervening seabed", to guide the boundary placement, and to provide inventories of the geodiversity captured (Harris, 2007). Geomorphic features thus represented the lowest spatial scale of physical surrogate used for reserve planning.

In all, 18 types of geomorphic feature were defined within the southeast region; the average size of features within types was highly variable, ranging from 12 to 179 800 km², and 80% of their combined area occurred in depths >1500 m (Table 1). Only 14 types occurred in the zone of importance (depths <1500 m). The two types making up most of this zone (55%) were the "undifferentiated" continental shelf and the "undifferentiated" slope; they therefore provided no additional data to the level above them (biome) in the hierarchial classification framework. This undifferentiated fraction, plus the area deeper than 1500 m, totalled 91%; therefore, differentiated features within the zone of importance made up only 9% of the total classified southeastern area. Most of this small fraction was made up of "terrace", "deep/hole/valley", "basin", and “plateau" feature types, differentiated largely by qualitative differences in seabed slopes (Harris et al., 2005).

Two feature types were particularly influential on the design process, because they were part of the design selection criteria (Anon., 2003): seamounts (pinnacles, sensu Harris et al., 2005) and submarine canyons. These made up <0.1 and 3% of the area of the zone of importance and, within this, had average areas of 12 and 69 km², respectively. These features were relatively well-defined, and identified in the reserve design process as being “special” types of geomorphic features (Harris, 2007).

Seamounts and canyons provide high prospective values as physical surrogates for biodiversity distributions. Seamounts have been described as “veritable oases of the deep” (Koslow, 2007), whereas enhanced plankton and nekton biomasses have been measured in and around canyons (Cartes et al., 1994; Genin, 2004). There may also be greater densities of benthic megafauna within canyons (Headrich et al., 1975; Cartes et al., 1994; Sarda et al., 1994; Vetter and Dayton, 1999), although this
pattern is not ubiquitous and may be taxon-specific or depend on
the type and quality of organic inputs (Schlacher et al., 2007).

Data source: submarine canyons and seamounts
Submarine canyons are abundant in the southeast region, relative
to other geomorphic features, but make up only a small fraction of
the total area (Table 1). Typically, they extend from the continental
shelf edge (canyon heads in ~170–200-m depths) to the abyssal
plain. Estimates of the total number of canyons vary, partly
because mapping is incomplete, and because no clear guidelines
were used to differentiate gullies, canyon systems, and mature
canyons (Greene et al., 1999; Goff, 2001). The mapping used for
reserve design in this region (Harris et al., 2005) revealed 100 indi-
vidual intersections of canyons with the zone of importance. An
updated mapping, using the best available bathymetry data avail-
able in October 2007, was used to calculate canyon sizes based on
the multibeam sonar (MBS) technology (Kloser et al., 2001, 2007).

Data on benthic invertebrate communities were derived from
video transects within nine submarine canyons (Zeehan, Arthur,
Ling Hole, Pieman, High Rocky, Big Horseshoe, Babel, Banks
Strait North, and Banks Strait South) collected on a number of
surveys in 2004 and 2005 (Williams et al., 2007a; Figure 2). Data
from Ling Hole canyon were excluded from this analysis owing
to obvious impacts on benthic fauna by commercial bottom
fishing. The video platform was towed down-slope from ~150-
to 500-m depth, 1–4 m above the seabed; camera depth and alti-
tude were recorded by a depth sensor attached to the platform.
The recorded videos were annotated at 1-s intervals for substratum
type, geomorphology, dominant fauna, and faunal abundance
(Kloser et al., 2004). The data from each tow were standardized
to percentage occurrence by 50-m depth-bins and averaged over
all canyons. For the results presented here, we simplified the faunal
classification into two categories: bare substratum and
rich fauna. Bare substratum included categories of no fauna,
bioturbators, and low abundance of other faunal types. Rich
fauna included medium and large abundances of “low encrusting”
and “mixed erect” faunal types, and small and large sponges. In
canyons, this was dominated by a low-relief (to ~30 cm high)
community of mostly small sponges and ascidians associated
with a diverse bryozoan assemblage (“bryozoan thicket”, sensu
Williams et al., 2007a).

Seamounts are also abundant in the southeast region, relative
to other geomorphic features (Table 1). The estimate of their
total number is, like canyons, uncertain because of incomplete
mapping and classification uncertainties. Maps used for reserve
design off southeast Australia revealed 11 seamounts/guyots,
plus 46 seamounts (classified as pinnacles by Harris et al., 2005),
south of Tasmania. Surveys in 2006 and 2007 incorporating
MBS detected an additional 102 (mostly small, but >2 km²)
seamounts south of Tasmania, raising the regional total to at least 159
(AW and RJK unpublished data). Data on benthic invertebrate
communities from 13 unfished and 9 fished seamounts are
derived from 17 and 16 video transects, respectively, completed
during the 2007 survey. The video collection and annotation
methods are described earlier, except that transects extended
from seamount peak to base (typically from ~900–1200-
to ~1600–1800-m depth). In some cases, transects extended some
distance beyond the seamount base, as defined by a gradually

<table>
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<th>Average feature area (km²)</th>
<th>Percentage of area (%)</th>
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<td>ZOI &gt;1500 m</td>
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<tr>
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<td>28</td>
<td>36 400</td>
<td>213 200</td>
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<td>43</td>
<td>186</td>
<td>546</td>
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</table>
| Knoll/abyssal-hills/hills.mountains/peak | 2
| Ridge                      | 0     | 5          | 0                         | 5 832                  | –                      | 1 166                  | 0                      | 1                      |
| Saddle                     | 0     | 2          | 0                         | 30 380                 | –                      | 15 190                 | 0                      | 3                      |
| Trench/trough              | 0     | 2          | 0                         | 2 082                  | –                      | 1 041                  | 0                      | <1                     |
| Abyssal plain              | 0     | 3          | 0                         | 539 400                | –                      | 179 800                | 0                      | 58                     |

Total (southeast region) 192 274 230 928 925 338 – – 20 80

Data are shown separately for the zone of importance (ZOI) for megafauna (continental shelf, upper and mid-slope in depths <1500 m), and depths >1500 m.
decreasing slope. The data from each tow were standardized to percentage occurrence in 100-m depth-bins and averaged separately for unfished and fished seamounts. Because all seamounts with shallow peaks (<1000 m) have been fished, comparative analysis of fishing impact is restricted to a depth range (1100–1300 m) common to fished and unfished seamounts. For the results of video-based analyses presented here, bare substratum is classified as for canyons, but rich fauna includes medium and large abundances of a variety of Octocorallia, Antipatharia, and sponges associated with accumulations of the reef-building scleractinian stony coral Solenosmilia variabilis.

**False homogeneity: depth**

The first way in which geomorphic features within a class were falsely considered as being equal relates to depth. Data from eight canyons reveal strong depth-related patterns in community composition (Figure 3a). Bryozoan thicket, the dominant community type around the canyon rims and canyon heads in

![Figure 3. Patterns of faunal distribution with depth, based on the percentage of video frames containing rich fauna vs. bare substratum in canyons and on seamounts in Australia's southeast planning region, (a) for seven 50-m depth strata along transects averaged for eight canyons; and (b) for seven 100-m strata averaged for 17 transects on 13 unfished seamounts.](https://academic.oup.com/icesjms/article-abstract/66/1/214/634078)
Australia’s deep-water reserve network

~150–350 m depths, is itself a surrogate for an exceptionally rich community of bryozoans (believed to exceed 100 mostly unidentified species; K. Gowlett-Holmes, pers. comm., November 2007) and an associated fauna of attached megafaunal organisms (predominantly sponges and ascidians; Williams et al., 2007b). The physical structure provided by rock terraces (~300–500 m), formed by the erosion of tertiary sedimentary rocks, provides refuges for mobile animals such as decapods (Williams et al., 2007a). This gives way to muddy sediments at greater depth (approximately >500 m) that support an extensive bioturbating fauna, evidenced by a high density of pits and burrows seen in images, but with little emergent fauna.

Data from 13 unfished seamounts south of Tasmania collected in 2007 also revealed a strong depth-related pattern in community composition similar to that of canyons, though over a different depth range (Figure 3b). Rich fauna (predominantly Octocorallia, Antipatharia, and sponges associated with accumulations of the reef-building scleractinian stony coral S. variabilis) decreased from nearly 90% of video observations in the 1000–1100 m depth stratum to zero below 1600 m. Bare substratum increased from 6 to 100% over the same depth range.

Depth-related patterns typify faunal distributions on the Australian deep continental shelf and slope, including those of benthic invertebrates (Koslows et al., 2001; Ponder et al., 2002) and fish (Last et al., 2005). This general pattern is captured in the hierarchical planning framework at Level 2, where biomes represent surrogates for depth-related faunal zonation. Our data strongly validate the use of biomic structure in the planning process. They also highlight a key facet of the hierarchical framework: faunal distributions are more fundamentally correlated with depth than with geomorphic features, and therefore geomorphic units and features need to be nested within biomes. Canyons, for example, typically extend across several biomes between the shelf edge and abyssal depths, whereas shallow seamounts typically extend from the mid- or lower slope depths (~700–2000 m) into upper slope depths (~<700 m). The nesting of physical features within depth is vital to using them successfully as surrogates, because the biodiversity captured is critically dependent on the depth range of the feature enclosed.

When only part of a feature is bounded by a reserve, it may be ineffective in representatively conserving biodiversity. Our data cover only the shallow depth range contained within reserves (to ~1800 m), and there are no data from comparable samples anywhere deeper in the Australian marine environment. Nonetheless, the data clearly demonstrate that the biodiversity captured in an individual reserve will considerably underrepresent benthic megafauna if the zone of importance is excluded. This will occur if, first, the features are too deep, e.g. canyons that do not incise the continental shelf edge or upper continental slope, or second, if only the deeper fraction of a whole feature is bounded by a reserve. Examples of both occur in the reserves of the southeast region, e.g. Nelson, Tasman Fracture, and East Gippsland (Figures 1 and 2).

**False homogeneity: size, complexity, and configuration**

Submarine canyons and seamounts modify local circulation patterns by interrupting, accelerating, or redirecting flows that are generally parallel with depth contours. The size, complexity, and configuration of the features determine the degree to which currents are modified and therefore their influence on local nutrients, prey, and potentially, benthic biodiversity (Roden, 1987; Vetter and Dayton, 1999; Allen et al., 2001; Wällin, 2002; Kämpf, 2005; Pattiaratchi, 2007; Pitcher et al., 2007).

Although the sizes, and to some extent the configurations, of canyons around southeast Australia can still only be estimated because the seabed is incompletely mapped, we re-evaluated canyon numbers and plan areas by incorporating the MBS data collected in the continental slope depth range (200–1500 m) since 2000, and using equivalent criteria for defining canyon features, as used by Harris et al. (2005). This demonstrates that the number of canyons in the original mapping, based on lower resolution MBS, was substantially underestimated (131 vs. 276), primarily because canyon heads were missed by the data available to the original mapping, which mostly came from depths >1500 m. In the Zeehan CMR, for example, the two canyons originally identified from deep-water bathymetry proved to be four (Figure 4; Kloster et al., 2007). Our new data demonstrate that canyon size range (estimated for depths <1500 m) varies considerably (Figure 5); most are small (<20 km²), whereas the four largest are 280–590 km². Only canyon features at the small end of the size range were captured within the southeast reserve network.

The Big Horseshoe canyon (Figure 2), the easternmost arm of the Bass Canyon system, is the largest southeastern canyon sampled for benthic biodiversity. It has a total area of 319 km² in <1500-m depth that supports a rich, abundant, filter-feeding benthic megafauna, including large sponges in dense beds of large individuals at 120 m and at 300–400 m, dense stands of the stalked crinoid Metacrinus cyaneus in 200–300 m, and many species of octocoral (especially gold corals) at depths >700 m (Kloster et al., 2001). The conservation value of this feature is highlighted by this being the type locality for M. cyaneus and its only known location off southeastern Australia. Current patterns from an Acoustic Doppler Current Profiler revealed an internal eddy present in this canyon during a survey in 2000 (Kloster et al., 2001), consistent with the hypothesis linking current modification with higher biological activity and diversity. Big Horseshoe, and the entire Bass Canyon system, remains outside the southeast CMR network.

In contrast, the three canyons within the Zeehan CMR (Figures 2 and 4) are relatively small, each <2.5 km² wide and with an average area of 34 km² shallower than 1500 m. Although there are no direct measurements of currents in these features, relatively low flows can be inferred from the composition of the benthic megafauna. Large sponges, crinoids, and octocorals were absent, and a low-relief bryozoan thicket (see previous section) was the only abundant megafaunal community present in 150–300 m depth. This contrast does not signify a lack of conservation value in the Zeehan CMR canyons; the sponge component is diverse and contains many rare but small species (Schlacher et al., 2007). The bryozoan thicket is vulnerable to removal by bottom trawling, a method of fishing which, outside the reserve network, occurs over much of the 150–300 m depth range (Wayte et al., 2006). In summary, these large and small canyons support different species and communities, with this variation mediated at least partly through the effect of feature size on local hydrodynamics.

Although this canyon comparison indicates a link between feature size and biodiversity, the correlation is confounded with other factors that also directly influence biotic distribution, in...
Figure 4. Map of submarine canyons showing canyon outlines identified in the initial mapping completed for reserve design (shaded polygons), overlaid on more recently collected MBS bathymetry in and next to the Zeehan CMR (broken boundaries).

Figure 5. The sizes of 276 submarine canyons in Australia’s southeast planning region, showing those wholly contained within a network of CMRs. Sizes based on GIS estimation of plan area for the portions of canyons in the zone of importance, depths < 1500 m (where the highest biodiversity conservation values and the greatest threats overlap). The four largest area-bins are considerably larger than the remainder.
this case, seabed bottom type and seabed slope. Much of the rich structural megafauna of the large Big Horseshoe canyon is associated with hard (rocky) substratum, which occurs on steep slopes where rock is exposed from surrounding muddy sediments (Kloser et al., 2001), whereas the smaller canyons in the Zeehan CMR are more gently sloping and mud-filled with less exposed rocky bottoms (Williams et al., 2007b). This difference may itself be related to current modification (higher currents restricting burial of rocky bottom in Big Horseshoe). It is not known whether the heterogeneity of seabed type and slope (complexity) is generally correlated with the size of canyons, or indeed other types of features. However, in the absence of mapping data, it is reasonable to expect that large features are likely to have great complexity, and will have relatively greater complexity than smaller features. Information on geomorphic substructure at finer scales (e.g. meso- and macrohabitat, sensu Greene et al., 1999), provided by video and inferred from MBS, will allow bioregional classification at lower levels in Australia’s hierarchical classification framework (Kloser et al., 2007). This has not been included in the reserve selection process in Australia to date.

False homogeneity: anthropogenic modifiers

A stated conservation goal for Australia’s NRSMPA is to capture biodiversity in a natural state (ANZEC, 1998). For benthic megafaunal diversity in offshore waters of the southeast region, the key direct threatening process is commercial fishing. Bottom trawling is the most prevalent fishing activity in offshore waters, and its direct impacts are removal of fauna, degradation of physical habitat, and changes to community composition (Williams et al., 2006; Smith et al., 2007). Trawling effort is widespread on the continental slope, where recent estimates (Wayte et al., 2006) reveal that at least 65% of the upper continental slope (200–700-m depths) and a large fraction of the mid-slope (700–1500-m depths) have been trawled in recent years. Trawling was concentrated on seamounts on the mid-slope, and is increasingly concentrated in canyons that are now accessible for bottom fishing, owing in part to improved navigational technology on fishing vessels (Williams et al., 2006). The benthic megafauna of the continental slope is regarded as particularly vulnerable to bottom fishing, because key elements such as corals are typically slow-growing and long-lived (some species are hundreds of years old; Stocks, 2004; Thresher et al., 2004). Fishing impacts on seamounts off southeastern Australia were documented by Koslow et al. (2001), who demonstrated that trawling could completely remove the benthic fauna; potential impacts on canyons include removal of fauna and degradation of physical habitats (Yoklavich et al., 2000; Williams, 2007b). Because these impacts can be long-lasting, or even permanent, where physical structures have been removed, it is important for reserve design to identify what the impacts are and where they have occurred.

Data collected from seamounts south of Tasmania in 2007 revealed that fished seamounts had a larger proportion of bare substratum (>65% cf. 7–32%) and a smaller proportion of rich fauna (<9% cf. 48–60%) than unfished seamounts in the depth range (1100–1300 m) common to all 22 seamounts surveyed (Figure 6). Shallower depth strata, including the peaks of shallow seamounts (~700–1000-m depths), were bare, consistent with the observations of Koslow et al. (2001). Initial data analysis also suggests that there has been little or no recovery from the impacts on fished seamounts that occurred more than a decade ago. Seamounts are therefore heterogeneous, based on fishing history. The reserve design requirement for conserving benthic areas in their natural condition was met off southeast Australia, because many (at least 121) individual seamount features discovered recently were included in the Huon and Tasman Fracture CMRs. This may not be the case in other planning regions, where fewer seamount features exist.

Discussion

False homogeneity

Where abiotic surrogates are used to represent biodiversity distributions, false homogeneity may result where sites with similar or identical abiotic conditions support different biological
distributions, but where those differences remain undetected (Stevens and Connolly, 2004). This was demonstrated from direct observations of benthic megafaunal invertebrate biodiversity for different depth zones on seamounts and canyons, for different sizes of canyons, and for seamounts with a different history of anthropogenic modification. False homogeneity was inferred for seamounts of different size, based on their different effects on local oceanography. At least two other factors, aggregation sites and between-feature connectivity, are likely to be important for biodiversity distribution and conservation. Geomorphic features, such as seamounts and canyons, provide biological aggregation sites. For example, in deep temperate Australian waters, the commercially fished orange roughy (*Hoplostethus atlanticus*) forms large spawning aggregations on a relatively small number of seamounts, guyots, and ridges (Bax *et al*., 2005), whereas the abundant basketnwerk eel (*Diastobranchus capensis*) forms spawning aggregations on only two of the 160 seamounts within its distributional range (AW, unpublished data). Although expert-based classification of abiotic variables as geomorphic features provides clear maps of geodiversity (*sensu* Harris, 2007), and was an important component of the design of Australia’s first deep-water marine reserve network, our results indicate that depth, size, complexity, anthropogenic impact, and other factors, such as aggregation sites and connectivity, need to be added as modifiers of the 21 geomorphic features proposed by Harris (2007) for Australia’s continuing MPA network design process.

Refinements and alternative approaches are possible, using the detailed bathymetry and substratum information collected by modern hydroacoustic equipment, in combination with wide-ranging and georeferenced image data from camera systems and other biological and environmental data (Kloser *et al*., 2001, 2007; Williams *et al*., 2007b). In the USA, Greene *et al*., (1999) used a detailed, spatially explicit classification that included biological attributes to describe two megahabitats of the Californian coast: Soquel submarine canyon in Monterey Bay and an area of the Big Sur coastline within the Big Creek Ecological Research Reserve. That classification was elaborated to include codes for attributes and has been applied successfully to many habitat-mapping projects in the USA, covering marine regions from the Subarctic to tropical latitudes, and from shallow waters to abyssal depths (Greene *et al*., 2007). Off New Zealand, 800 known seamounts (discrete bathymetric features with at least 100 m of relief) were categorized using 16 environmental variables ranging from latitude and water mass to depth and elevation (Rowden *et al*., 2005). Multivariate classification analysis led to 12 groupings, distinguished primarily by four variables, depth at peak, depth at base, elevation, and distance from the continental shelf. Classification of seamounts based on ecological criteria generally increases the number of categories when compared with strictly geological criteria (Pitcher *et al*., 2007).

### Lessons from the southeast reserve network

Given the lack of knowledge of distributions of a complex and varied biodiversity in Australia’s southeast region, and the 2012 target for completing the national network (the NRMPA), feature-scale geomorphic surrogates were successful in providing a full, contiguous regional mapping in a suitable timeline and allowing some key localities to be identified. However, a consequence of using non-validated surrogates and not differentiating features within a class (false homogeneity) is that the final outcome for biodiversity remains unknown. Evaluating the result using an inventory of geodiversity (Harris, 2007) may reveal that representative geology has been captured, but it fails to differentiate between large and small biodiversity gains. Capturing large areas or large numbers of features that do not correspond to areas of important biodiversity is likely to mask deficiencies in the true conservation outcome. Minimizing socioeconomic impacts is a stated management goal for reserves (Anon., 2003), and the highest risk from masking is missing biodiversity in the zone of importance, where anthropogenic activity is great. This is realized in the southeast region, where the collective area of reserves in <1500-m depth is <10% of the total (Table 2).

Collectively, these observations indicate that reserve designs that use geological features in bioregional classifications will benefit from refinements. The primary need is to validate abiotic surrogates of biological distributions and biodiversity values, thus allowing types of geomorphic features, or units, to be objectively differentiated (true heterogeneity), and features within types to be classified using relevant modifiers (true homogeneity).

The above approaches have the disadvantage that they divide deep-sea habitat *a priori* into categorical units (types), whereas experience tells us that biodiversity is distributed continuously (Samadi *et al*., 2006). If differences in biodiversity between selected geomorphic features were recognized as being not absolute but rather proportional, many different options for spatial management for conservation purposes would open up.

Defining abiotic surrogates, independent of biological information, is only one approach to developing them. An alternative approach is first to define the patterns in biodiversity, then to find abiotic variables that can best explain these patterns. This approach has the advantage that it starts by defining the object of interest (biodiversity), but suffers from some of the same disadvantages of the geomorphic-feature approach in that there may be little correspondence between the scale and patterns in biodiversity and those of the abiotic variables, which will ultimately be needed to predict patterns in biodiversity for areas where biological data are limited. It also places a great emphasis on the need to define patterns in biodiversity clearly, which can be difficult in the deep sea, where sampling is typically limited, samplers typically selective, and different faunal groups will have very different patterns (and scales) of distribution.

A third approach would be to define patterns in biodiversity and abiotic variables jointly. This offers the advantage of providing a classification that preserves the maximum information of both datasets, thereby maximizing the potential for predicting patterns

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### Table 2. Plan area (km²) and percentage of depth zones (biomes) included within the southeast network of deep-water CMRs (SE CMRs), showing the zone of importance (where the highest biodiversity conservation values and the greatest threats overlap) and greater depths.

<table>
<thead>
<tr>
<th>SE CMR network</th>
<th>Zone of importance</th>
<th>Deeper (&gt;1500 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inner shelf (&lt; 100 m)</td>
<td>Outer shelf (100–200 m)</td>
</tr>
<tr>
<td>km²</td>
<td>9 896</td>
<td>5 284</td>
</tr>
<tr>
<td>%</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>
in biodiversity from abiotic variables. A joint definition would require that both sets of data are retained as continuous variables to the extent possible; as soon as data are categorically classified, information will be lost and an artificial structure imposed that may not be matched by the structure in the corresponding dataset. Geologists, biologists, oceanographers, and others need to work together to develop a common understanding and characterization of the structure and patterns in deep-sea biodiversity and the processes that formed and maintain them.

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