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A hierarchical framework for classifying seabed biodiversity with application to planning and managing Australia's marine biological resources

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ABSTRACT

A conceptual hierarchical framework for classifying marine biodiversity on the sea floor, used successfully for continental-scale bioregionalisation and adopted to guide marine resource planning and management in Australia, has wider application at a global scale. It differs from existing schemes for classifying marine biota by explicitly recognizing the overarching influence of large-scale biodiversity patterns at realm (ocean basin and tectonic), provincial (palaeohistorical) and bathomic (depth-related) levels. The classification consists of 10 nested levels within realms, of which the first seven are primarily spatially nested and ecosystem based, and the lowest levels represent units of taxonomic inheritance: 1 – provinces, 2 – bathomes, 3 – geomorphological units, 4 – primary biotopes, 5 – secondary biotopes, 6 – biological facies, 7 – micro-communities, 8 – species, 9 – populations, and 10 – genes. According to this scheme, marine biodiversity is characterised in a systematic way that captures the scale-dependence and hierarchical organization of the biota. Levels are defined with respect to their functional roles and spatial scales, in a manner that directly supports the incorporation of biodiversity information in regional-scale planning by highlighting centres of endemism, biodiversity richness and priority information needs. Whereas species are the fundamental units of biodiversity, biological facies are the smallest practical unit for conservation management at regional scales. In applying the framework we make extensive use of biological and physical surrogates because marine data sets, particularly those of the deep sea, are usually sparse and discontinuous. At each level of the hierarchy, attributes and surrogates are defined to reflect the scale and range of biogeographic and ecological processes that determine the spatial and temporal distribution of marine biodiversity. The Australian experience in applying this framework suggests that it provides a workable systematic basis for defining, managing and conserving biodiversity in the sea.

1. Introduction

Studies of marine biodiversity have focused almost exclusively on local-scale processes which are typically less informative than biogeographic processes for understanding species richness patterns (Gray, 2001). While ecosystem-based management (EBM) of marine systems aims to manage biota at continental and broad regional scales, knowledge of large-scale biodiversity is usually poor. In such circumstances, biodiversity surrogates, based on more easily mapped geophysical variables, are an attractive option for representing biological patterns (Zacharias and Roff, 2000). However, the use of physical surrogates in isolation has often meant that the relevance of, and context provided by, mega-scale biodiversity have been overlooked. When the geographic scale of a bioregion includes a whole continent, knowledge of the fundamental aspects of biodiversity, such as its biogeographic structure, is essential for management planning. Nevertheless, incorporating the biogeography of marine biodiversity at national scales has not been approached systematically (Roff, 2005).

The classification of biodiversity into hierarchical units is not new (Noss, 1990; Soberon et al., 2000). Various hierarchical ecological approaches have been proposed to conserve terrestrial (Noss, 1990) and marine biodiversity (Zacharias and Roff, 2000). However, most approaches focus on the lower and middle levels of biodiversity (i.e., genes, populations, species and communities) and rarely deal with larger, meso- and mega-scale units (i.e., realms based on ocean basin tectonics, biogeographic provinces based on evolution, and bathymetric associations based on depth) that encapsulate historical patterns in biodiversity and the processes driving its distribution. Harding (1997) provided a four tier, mega-scale classification of marine biodiversity but did not attempt to link his hierarchy to lower (biocoenotic) levels. Spalding et al. (2007) have since summarised existing national regionalisations to produce an amalgamated set of realms, provinces and ecoregions, covering all coastal and shelf waters of the world. The maps were derived through qualitative reinterpretations of existing national regionalisations, based on three principles: "that

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it should have a strong biogeographic basis, offer practical utility, and be characterised by parsimony". Their hierarchy was chosen to be parsimonious with apical elements of a preliminary framework which formed the basis of an Australian provincial regionalisation reported in IMCRA (1998), but developed in an earlier scientific analysis (Anon, 1996a). Our framework was constructed to integrate all of these levels, focusing on improving their utility for managing biodiversity at continental-scales. A top-down approach was used to classify biodiversity within a sequence of nested levels (below the scale of realms) that reflect the processes that drive/determine each level. In the absence of a complete regional coverage of biological data, biodiversity surrogates were used to appropriately assign biological, geological and physical information to each level. This approach allowed us to deal with biogeographic complexity and to selectively reduce entropy by appropriately combining biological and geophysical information.

Biodiversity, with both biotic and abiotic components, includes the variation of life at all levels of biological organization (Gaston and Spicer, 2004). However, it can and has been interpreted in many ways (Noss, 1990; Ray, 1996), often reflecting disciplinary biases and confusion of the issues of scale and context. For example, ecologists and mangers concerned with processes typically focus on mid-levels of biodiversity, whereas biogeographers focus more on larger regional scales, and taxonomists and molecular biologists focus mainly on the basal levels of biodiversity – the species. In practical terms, these levels form part of a natural hierarchy being either fully or partially nested in levels above and providing quite different information in a biodiversity management context. Consequently, discussions about biodiversity are often incoherent because participants, focusing on different levels of the hierarchy, are often at cross-purposes.

The effectiveness of marine resource management practices depends largely on the complexity and knowledge of a region and the strategies employed. An initial step must be to scope the region's biodiversity. In biogeographically complex regions, faunas should be classified initially into smaller, more manageable units to assist with this process. Our framework was designed and tested over more than a decade to produce bioregionalisations of Australian seas, and to assist development of broad-scale regional management plans and strategies for conserving and preserving biodiversity. The continental-scale, Australian marine domain has one of the most diverse biotas on the planet (IMCRA (1998)) so this provided serious challenges. These included describing the province-level biogeographic structure of the region to highlight core features of its biodiversity.

This paper introduces a unified, hierarchical framework for describing the structure of marine biodiversity across all spatial scales from global/oceanic realms to genes. We provide the rationale for this framework and describe key features of the various levels. Its application to the Australian Marine Jurisdiction in the context of Australia's Oceans Policy, including the implementation of bioregional marine plans and a representative system of marine protected areas, is discussed. We highlight issues that require further clarification, in terms of scientific and policy interpretation, and suggest priority areas for further research in terms of the fundamental assumptions underlying the framework. Notwithstanding the need for this additional work, we consider that the framework constitutes a significant step towards EBM of marine systems with broader application in a global context.

2. Bioregionalisation of Australian seas

The "island continent" of Australia is surrounded by marine habitats covering more than 11 million km^2 of seafloor in three oceans (Williams et al., 2009). It has one of the most diverse marine biotas on earth, extending from cool temperate seas in the south to tropical seas in the north. Seabed environments are represented by a rich and diverse array of habitats, and the fauna is a commensurately complex mix of organisms of recent and ancient origins displaying unusually high levels of micro-endemism.

Conservation of Australia's biodiversity is a key environmental responsibility under a suite of strategies and obligations that include the Convention on Biological Diversity (UNEP, 1994), the national strategy for Ecologically Sustainable Development (Anon, 1992b), the national Strategy for the Conservation of Australia's Biological Diversity (Anon, 1996b), and the 2002 World Summit on Sustainable Development. A key expectation of these commitments is the establishment of a National Representative System of Marine Protected Areas (NRSMPA) by 2012. Yet, despite these responsibilities, prior to 1996, knowledge of the large-scale structure and distribution of the biota, required for sound management of biodiversity, was either patchy or lacking. Data gaps are particularly problematic in a large and complex region such as Australia where much of the biota remains undiscovered, or has not been formally identified and named.

The hierarchical framework adopted, starting with large biogeographic scales and working progressively to finer, nested scales, allowed us to define Australia's biogeographic regions as a key input in marine conservation planning and ecosystem management (Commonwealth of Australia, 1998). This approach, whereby biodiversity is classified into nested levels, enabled a complex fauna to be subdivided, sequentially, making use of geophysical surrogates but retaining biological authenticity. A prototype scheme, developed for classifying seabed biodiversity, was originally used for an interim marine bioregionalisation of Australia (Anon, 1996a), and later revised for environmental management planning for northwestern Australia (Lyne et al., 2006). It has been adopted in evolving forms for a variety of similar regional studies (e.g., Butler et al., 2001; Commonwealth of Australia, 2005; Last et al., 2005), but the rationale, application and limitations of the approach have not been formally documented in the primary literature. This approach, which now forms the biological basis of Australia's Bioregional Marine Planning (BRMP) (formerly Regional Marine Planning, RMP), was adopted after critical review by leading federal and local (state) conservation scientists, as well as by an active national marine bioregionalisation committee, overseeing the marine regionalisation process. Considerations in implementing the approach are explained below using selected examples from national regionalisations of Australian seas and a regional investigation of the biodiversity of the continental margin of southeastern Australia.

3. Hierarchical classification of seabed biodiversity

Contemporary marine biotas exhibit distributional patterns based on ancient evolutionary processes (Ricklefs, 2006). Oceanic realms, often recognised as the largest marine geographic subdivisions, have been interpreted as mega-scale evolutionary units (Kauffman, 1973; Briggs, 1995). They differ from Large Marine Ecosystems (LME's) which can be viewed as largely geopolitical units, often lacking a biogeographic basis (Sherman et al., 1995). Various schemes, that equate large-scale, 'apical' biotic units to ocean basins and continental plates, have been proposed (Schmidt, 1954; Briggs, 1974; Pielou, 1979). The Australian continent and its marine domain belong to a large oceanic realm, which includes adjacent geopolitical regions New Zealand and New Guinea, united by their co-occurrence on the eastern sector of the Indian–Australian Plate (Hall, 2001).

Although details of the geophysical evolution of the Indian–Australian Plate remain subject to some debate (e.g., Handayani, 2004), it is clear that large-scale tectonic processes have profoundly shaped the Australasian marine environment and evolution of species along its margins (Hall, 2001). Key processes in this respect include vicariance and dispersal events following the fragmentation of Australia from Gondwana, mediated by oceanic processes and warming during its northward drift. This includes subsequent connection and mixing with the faunas of Asia and their southward dispersal along the eastern and western Australian margins, and later remixing in the north brought about by the opening of the Indo-Pacific passages through sea level rise (Last et al., 2005). The relative isolation and unique evolutionary environments have resulted in a higher degree of endemism in the southern inshore biota compared to those of the north (Wilson and Allen, 1987; Anon, 1996a). Given the historical complexity of the Australasian region, conservation planners needed a biogeographical framework that would include the key patterns of evolution imprinted in the contemporary fauna. Within that framework, geological, geomorphic and/or physical oceanographic surrogates could validly provide information at mid-levels of biodiversity where direct biological evidence is unavailable or unclear.

In our conceptual framework, continental-scale marine biodiversity is encapsulated in 10 nested hierarchical levels (i.e. below the level of oceanic realm) to describe the spatial structure of the biota (Fig. 1). The seven upper levels of the hierarchy, reducing from biogeographic provinces to micro-communities, are ecosystem based; the three basal levels are species-based and include species, populations and genes. The use of hierarchical schemes, and the role of scale in defining contemporaneous biodiversity, has been recognised in a number of studies (Allen and Starr, 1982) but these do not take account of the role of processes in space and time. As a general rule, collections of endemic species that have co-evolved in a unique way over geological eras are characteristic of the uppermost levels of biodiversity. These units generally have large spatial scales but there are exceptions. For example, collections of micro-endemic species, isolated within relatively small but unique geophysical environments (e.g., the Gulfs of South Australia and Port Davey in Tasmania – see Anon, 1996a), are represented at much smaller-scales more typical of units at levels below.

Different sorts of information are embedded within each level of the hierarchy, so data intrinsic to each level must be interpreted judiciously. Some levels contain only biotic or abiotic information, others a combination of both. Hence, the nested levels of our scheme are each characterised by unique, interacting ecological processes at a range of temporal and spatial scales. These units of biodiversity, the processes that determine them, and their relevance to regional-scale planning, are described below:

3.1. Level 1. Biogeographic provinces

Evolutionary biogeography, which identifies patterns of endemism and co-evolution at plate tectonic scales and below, is the key process at this level. The primary sources of endemism are along or within the boundaries of collision, subduction, upheaval, or separation of plates or water masses. These events are followed by dispersal, colonisation and speciation that collectively define the broadest spatial scale of local endemicity denoted here – the province level. Thus, the implicit assumption is that unique and/or shared biogeographic and evolutionary processes have determined broad centres of endemism that are inherent in the patterns of biodiversity at provincial scales. In practice, provincial units are primarily determined from micro-endemic species and the shared distributional ranges of co-evolved species (biogeographically informative species). In the extant Australian marine biota, these species are the products of palaeohistorical events, often asynchronous, and possibly spanning more than 100 mya (Wilson and Allen, 1987).

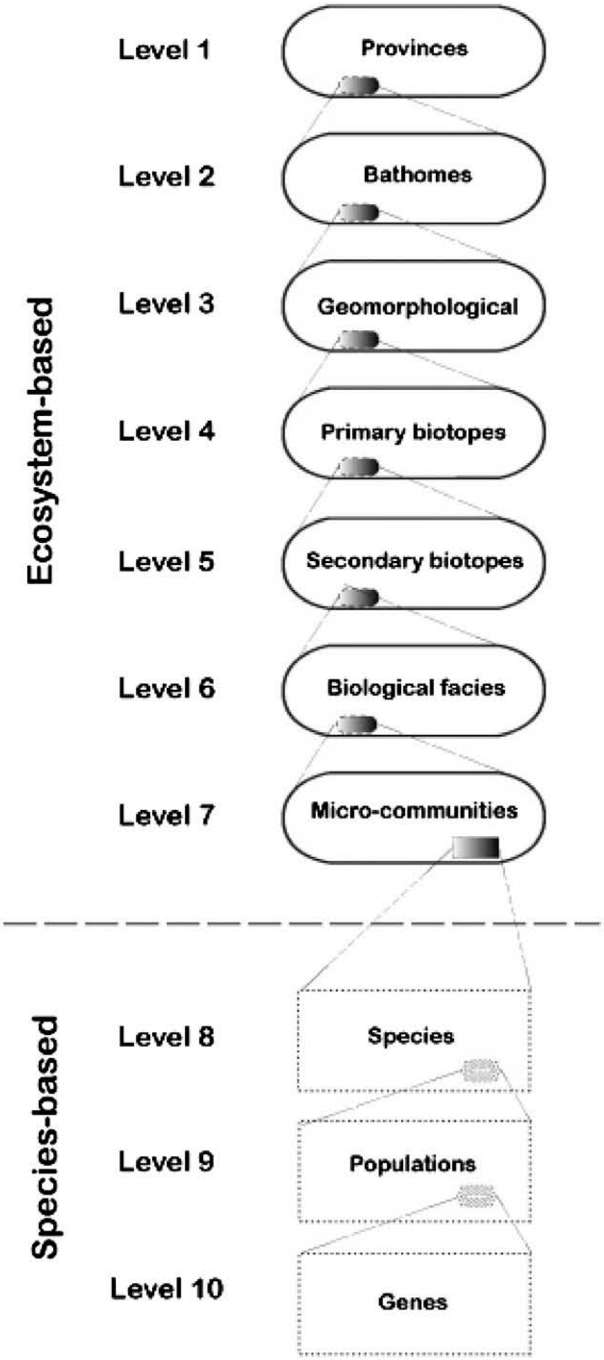


Fig. 1. The conceptual hierarchical framework used for classifying seabed biodiversity as applied to marine resource planning and management in Australia. It shows the 10 nested levels existing within an ocean realm.

Biogeographic provinces have a unique biotic composition and structure. However, factors affecting their origins differ. The distribution of biotas along the continental slope can be determined by major geomorphological structures or barriers. For example, the otherwise wide-ranging, continental slope biotas of northwestern Australia and Indonesia are faunally distinct because deep trenches restrict dispersal of species with poor larval and adult dispersal mechanisms (Last and Séret, 1999). Similarly, stenobathic continental slope species occurring in the deep basins surrounded by shallow water, such as the Sulu Sea in the Philippines, harbour disproportionally high levels of endemics (Compagno et al., 2005). The temperate inshore Australian biota has complex provincial structuring across southern Australia (Whitley, 1932; Anon, 1996a) that is largely attributed to recent evolutionary events, caused largely by rises and falls in temperature and sea level. Also, inshore provinces seem to be more significantly impacted by 'recent' climatic events than equivalent deepwater units on the continental slope.

In the marine bioregionalisation of Australia, province-level structure was determined largely by modelling the distributions of fish species from the Australian continental shelf (Anon, 1996a) and slope (Last et al., 2005). Fishes acted as surrogates for marine invertebrates and plants because reliable spatial data were initially unavailable for these groups at a continental-scale – recent work has confirmed similar distributional patterns in six megabenthic invertebrate groups off Australia's western margin (Williams et al., 2010). Nine province-level units were identified on the continental shelf (Fig. 2A), and an additional eight units on the continental slope (Fig. 2B). These large-scale units, characterised mainly by suites of co-occurring, narrow-ranging endemics, are separated by equally broad transition zones demarcating regions of biotic overlap referred to as biotones (or zootones when referencing the fauna). Provinces and their biotones, collectively referred to as ecoregions by Spalding et al. (2007), were used to construct planning frameworks for the whole Australian EEZ (Commonwealth of Australia, 2005, 2006). Artificial boundaries dividing management zones were usually placed within biotones, rather than through provinces, to ensure that unique features of a province were captured fully; in all, five regional marine planning regions were identified. The advantage of this approach over geographic, political or delphic regionalisations is that the province-based, Bioregional Marine Planning (BMP) framework has a solid biodiversity basis.

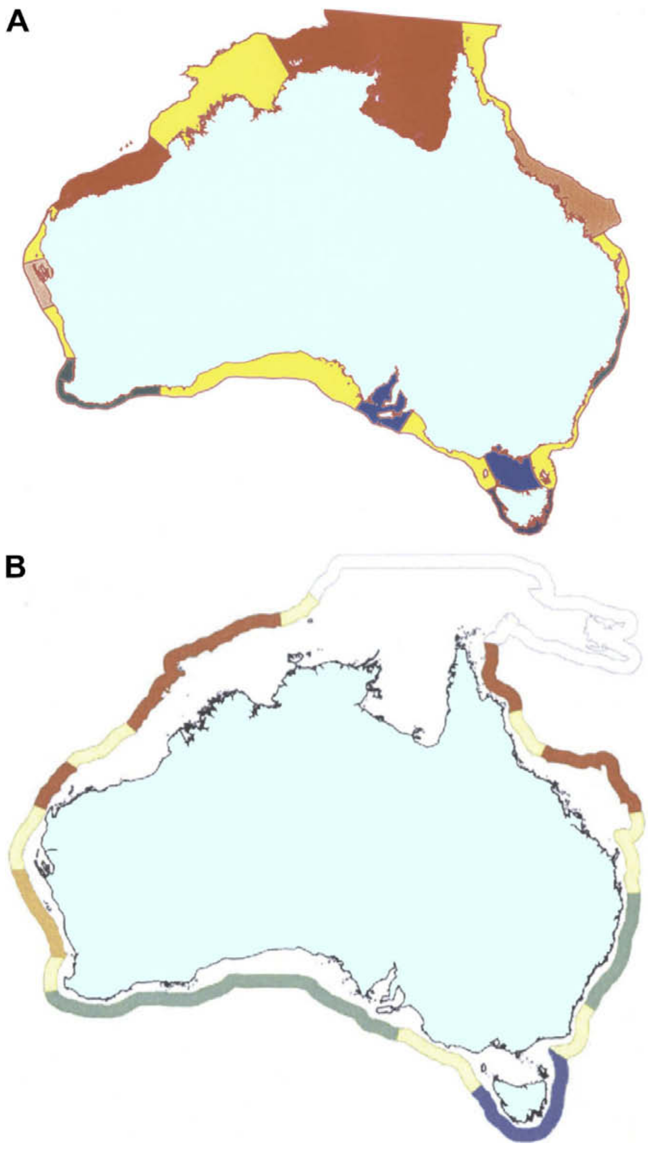


Fig. 2. Province-level regionalisation of the Australian benthic marine environment based largely on the distribution of fishes: (A) continental shelf (after Anon, 1996a) and (B) continental slope (after Last et al., 2005). Transition zones are depicted in yellow; province-level units in red (tropical), pink (subtropical), green (warm temperate) and blue (temperate). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Provinces and their associated transition zones also represent different elements of the biota and this has important implications for marine protected area (MPA) selection. A key objective for conserving biodiversity is ensuring that local endemicity is adequately represented. Biotones, as regions of biotic overlap, typically contain mixtures of species from adjacent provinces and can be more species-rich than their associated provinces. However, biotones typically have fewer unique species, and unique species at relatively high abundance, and therefore do not represent vulnerable and range-restricted (local) endemics as well as biogeographic provinces. In MPA selection algorithms, care must be exercised in using criteria based on species richness alone, as province-level biodiversity is more appropriately represented by endemism. MPAs should be at least partly located within province boundaries to adequately capture and conserve the uniqueness of their biodiversity.

In Australia, the spatial scale of provinces is in the order of 23,000–1,390,000 km^2 with sizes varying across biogeographic regions depending on their palaeohistory and evolutionary complexity. In the south-east, the cool temperate shelf fauna is represented at this level by two provinces (the Bassian and Tasmanian Provinces) separated to the north from warm temperate provinces (the Central Eastern and Gulfs Provinces) by biotones in the north-east and north-west, respectively (Anon, 1996a). An illustrated example, using the seamount fauna off southern Tasmania in the Tasmanian Province, demonstrates nesting within the hierarchy from Levels 1–6 (Fig. 3).

Typical units: province-level biogeographic assemblages (see Fig. 3A).

3.2. Level 2. Bathomes

Depth is the strongest environmental correlate of fish community structure in deep Australian marine environments (Williams and Bax, 2001; Last et al., 2005; Ponder et al., 2002). Bathomes, also variably referred to as environmental regions or zones (Hedgepeth, 1957; Last et al., 1983; Nybakken, 1997), and in an Australian context as marine biomes (Anon, 1996a; Last et al., 2005), are finer-scale subdivisions of provinces that are characterised primarily by the bathymetric distribution of the biota. We propose a new term bathome, in preference to biome, to avoid confusion with much larger-scale, pelagic-based, global marine units as defined by Longhurst (1998). The governing factors at this level are temporally evolving, depth-related processes (e.g., depth-layering of water masses), contemporaneous physiological constraints on species depth distributions, and depth-related differentiation in habitat distribution defined by geophysical constraints, all of which have affected the evolution of the biota. Like provinces, the spatial scales of bathomes are large (usually exceeding 1000 km^2 and much larger at abyssal depths) compared to units at lower levels of the hierarchy. Provinces, bathomes, and their associated

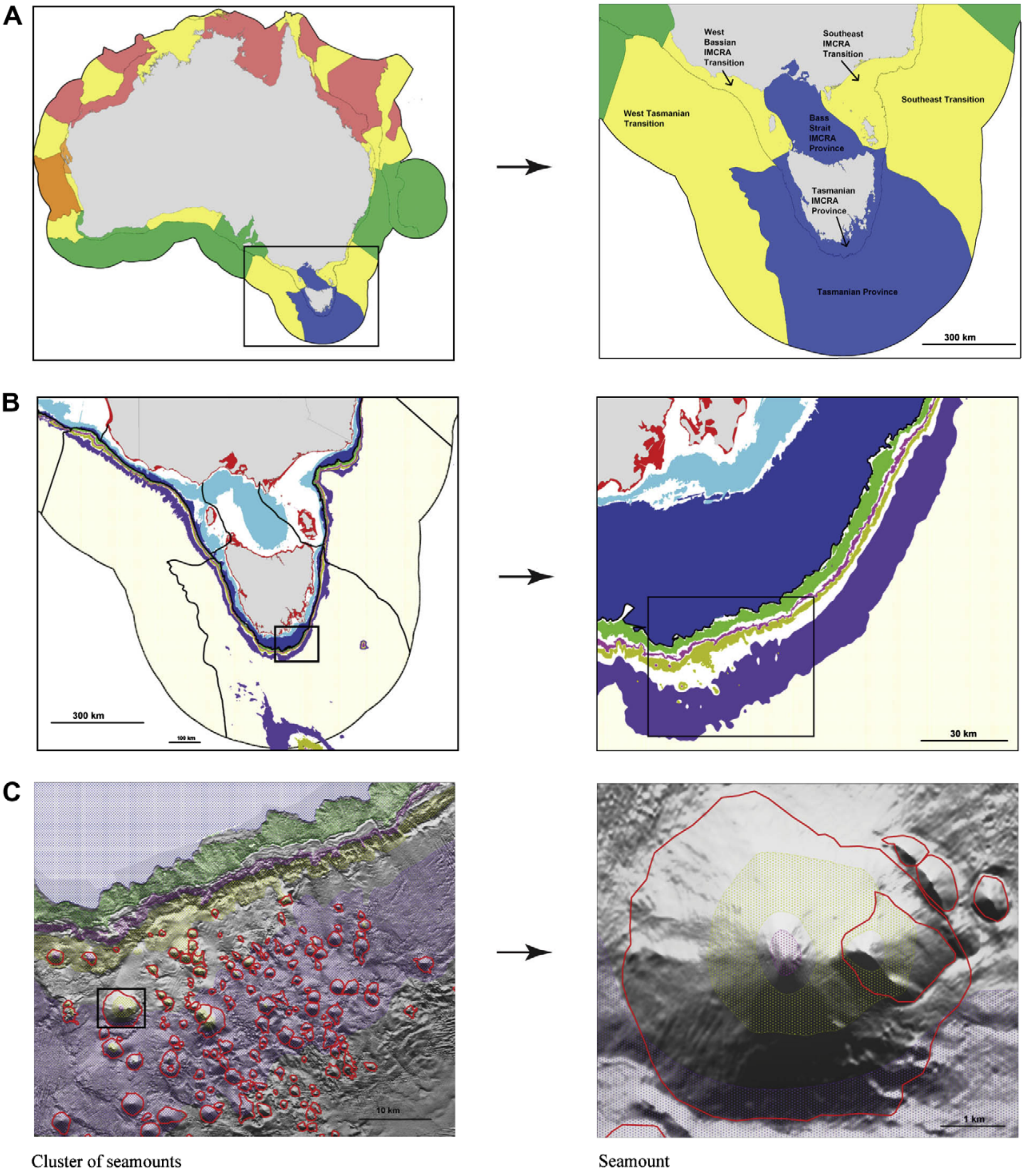
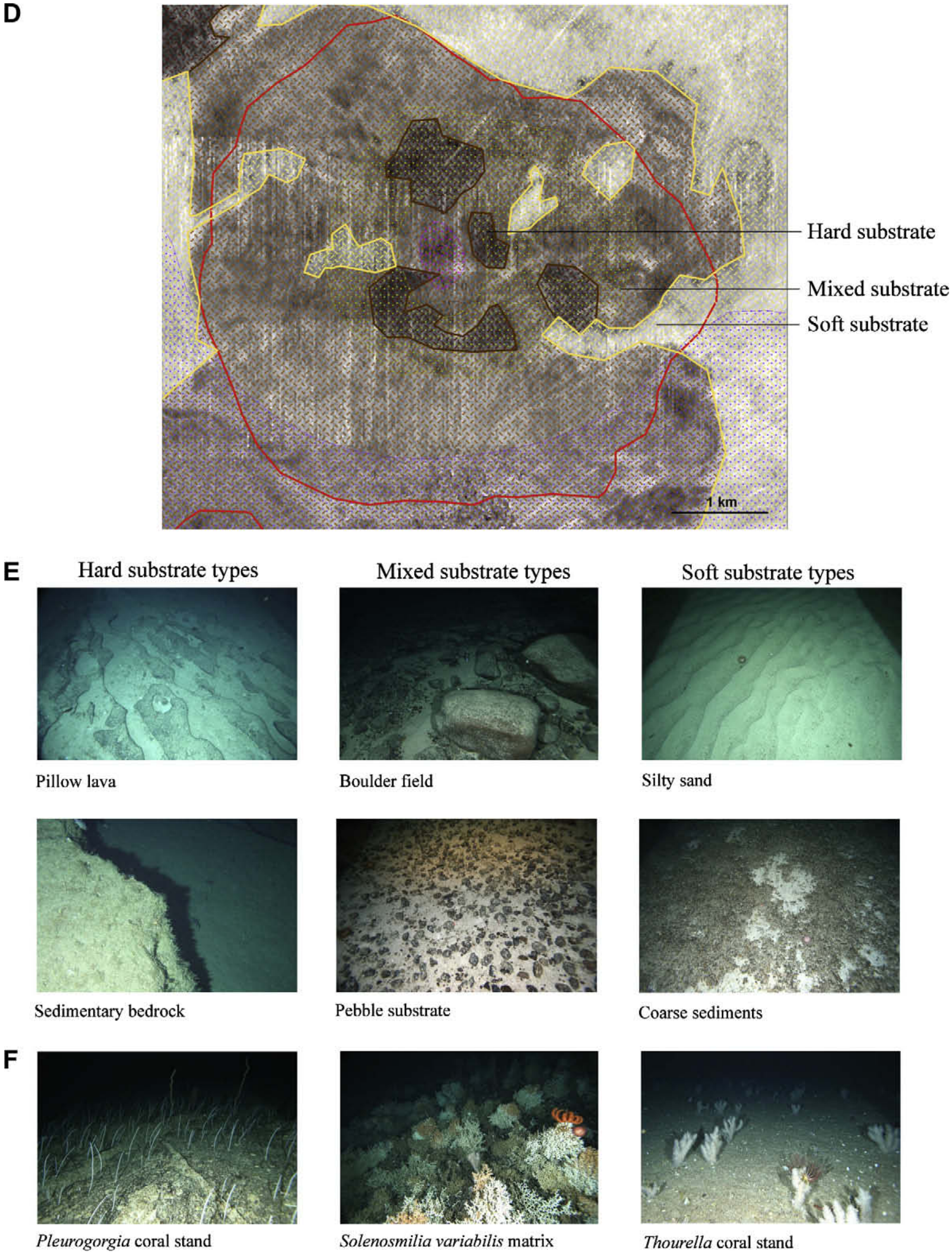


Fig. 3. Illustrated example showing how the six upper levels of the hierarchical framework can be used to identify biodiversity distribution within an area of the South-East Australian marine planning region. (A) Level 1: Provinces – recent national-scale mapping of provinces on the Australian continental margin provides context for the zoom-in view of the cool temperate Tasmanian province and adjacent transition zones, (B) Level 2: Bathomes – SE regional-scale mapping of bathomes defined with bathymetric boundaries, with zoom into southern continental slope, (C) Level 3: Geomorphological units – a large cluster of small seamounts on the mid-continental slope, with zoom into an individual geomorphological feature (Pedra Seamount) with stippling showing how a single feature may be nested within multiple bathomes, (D) Level 4: Primary biotopes – delineation of seabed into hard, soft and mixed substrate types based on backscatter mapping using multibeam sonar (Pedra Seamount), (E) Level 5: Secondary biotopes – resolution of substrate types using photographic imagery, and (F) Level 6: Biological facies – examples of biological facies of seamounts.

transitions, are continuous throughout a region, unlike lower level units which are spatially disjunct and patchy.

The sea has been divided by ecologists (e.g. Lincoln et al., 1998) into neritic and oceanic zones with the boundary between them demarcated at the continental shelf margin (i.e. the shelf break) – defined typically by the 200 m isobath or the point of greatest gradient change between the shelf and slope (Fig. 4). The neritic zone has four primary subdivisions, the estuarine, coastal marine, demersal shelf and inshore pelagic bathomes. The oceanic zone consists of three primary demersal subdivisions, bathomes of the continental slope (bathyal), abyssal, and hadal zones, and five primary pelagic subdivisions, bathomes of the epi-, meso-, bathy-, abysso- and hado-pelagic zones. Because the biotic compositions of demersal bathomes are typically different to each other, they



Pillow lava

Boulder field

Silty sand

Sedimentary bedrock

Pebble substrate

Coarse sediments

Pleurogorgia coral stand

Solenosmilia variabilis matrix

Thourella coral stand

Fig. 3 (*continued*)

need to be treated as independent ecological units. In comparison, pelagic bathomes exhibit greater spatial overlap, in main part because the distributional ranges of pelagic species are typically more extensive (Lyne and Hayes, 2005). Also, many oceanic fishes are eurybathic, undertaking extreme diurnal vertical migrations across bathomes during their night-time ascent for feeding (e.g., Williams and Koslow, 1997).

While primary bathomes provide a useful way of categorising biota, they can be further subdivided, based on their biological composition, to reflect finer scale, depth-related substructure. For example, on the northwestern Australian continental shelf, demersal fishes and benthic invertebrates are distributed in distinct inner-, mid- and outer-shelf assemblages (e.g., Lyne et al., 2006). Similarly, continental slope fishes are consistently partitioned into at least three demersal assemblages (Fig. 5) in each Australian marine province (Last et al., 2005) where they more-or-less conform to upper slope (275–500 m), mid-upper slope (630–775 m), and mid slope bathomes (870–1100 m). Limited survey data suggest that at

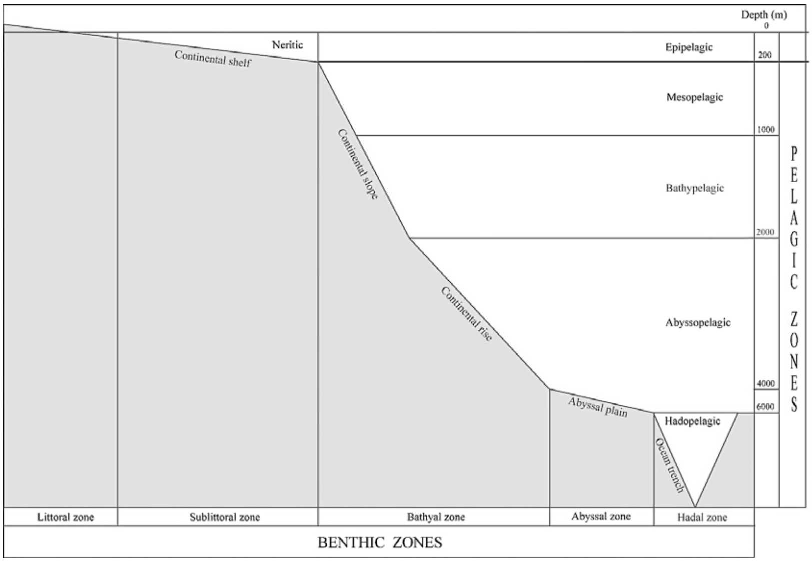


Fig. 4. Primary bathomes of the sea (after Lincoln et al., 1998) showing pelagic and benthic zones; in the Australian context, multiple bathomes exist on both the continental shelf and slope.

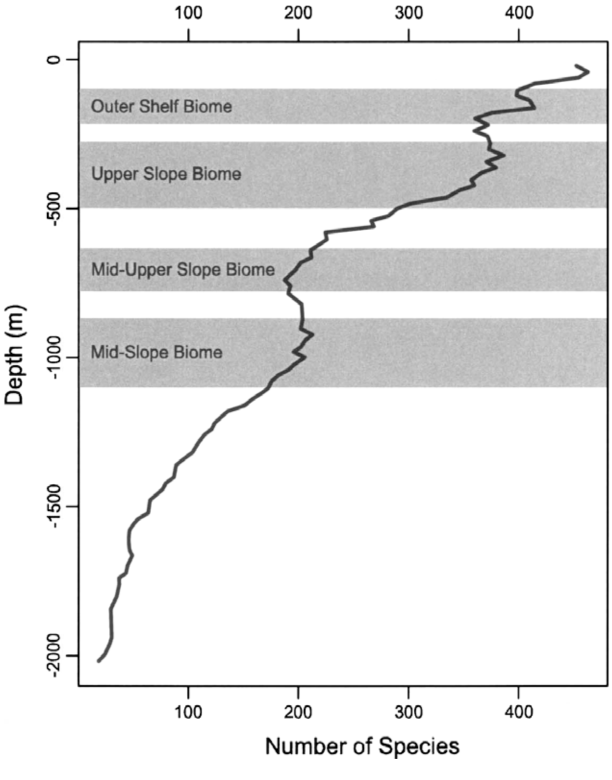


Fig. 5. Bathomic structure of demersal fishes on the continental slope of Australia (after Last et al., 2005).

least one additional, undefined bathome exists on the lower continental slope off Australia (i.e., from about 1400–2000 m).

Like transition zones between provinces (biotones), the transitions between biological communities at the lower levels of biodiversity (ecotones), are rarely sharply demarcated. Ecotone size on the sea floor depends largely on the physical environment of adjacent bathomes. For example, an ecotone on a gently graded continental slope will usually be broad. In contrast, steep bathymetric contours breaching two adjacent bathomes and separated by a small ecotone, can produce more strongly demarcated faunal disjunctions.

Bathomes are important large-scale units of marine biodiversity because the composition and structure of their assemblages differ markedly within a province, and elements of the same bathome typically differ between provinces. While some elements of a province are shared between bathomes (i.e., eurybathic species), others show strong affinity to a particular bathome (i.e., stenobathic species). Few demersal species occur in the coastal bathome as well as in continental slope bathomes, although fishes undertaking ontogenetic cross-shelf migrations are exceptions. In summary, bathomes are useful surrogates for capturing depth-related community structure within provinces.

Typical units include: estuarine, coastal, continental shelf, continental slope and abyssal bathomes (see Fig. 3B).

3.3. Level 3. Geomorphological units

Bathomes can be partitioned further into Level 3 mesoscale units, typically smaller in size, based primarily on geomorphology, and defined by abiotic characteristics. Geomorphological units are mappable structures, which are usually easily identifiable from each other, and are assumed to be surrogates for distinctive biological assemblages responding to ecological niches provided by aspects of their physical environment. These surrogate relationships are well documented for some geomorphic units such as estuaries, but remain largely unvalidated for others, e.g., many of those differentiated in the deep sea (>200 m depth) (e.g., Heap and Harris, 2008). Thus, Level 3 units typically act as surrogates for suites of assemblages at intermediate spatial scales.

Strict nesting of geomorphological units within levels above is necessary when applying this level of the framework to biodiversity management. This requires recognizing that the same geomorphological units within a province–bathome combination should have a similar array of biological components, but two Level 3 units in the same class (e.g., submarine canyons) located in different provinces, will usually have quite different biotas. Similarly, while geomorphological units may nest conveniently within a single bathome, there are exceptions. For example, a canyon extending down the continental slope will typically extend through a broad depth range crossing multiple bathomes. In such instances, the area of the geomorphological unit, the canyon, may exceed the scale of individual bathomes of which it forms part. However, by definition, each bathome has a unique biological assemblage based on depth, so each bathomic layer in the canyon should have a biotic composition distinct from those adjacent. Thus, the geomorphological unit 'canyon' consists of multiple Level 3 units that are nested in depth intervals defining the bathomes (i.e., canyon – upper slope, canyon – mid slope, etc.). It is only within an ecosystem context, where habitats and functional groups are linked together by a common set of oceanographic processes, that the canyon is usefully treated as a single entity. To do so involves the integration of pelagic and demersal classifications within a systems perspective (the subject of a future paper).

In the Australian context, accurately identifying and mapping geomorphological units in each bathome of each province was found to be a critical initial step for identifying key elements of the region's biodiversity. This process identifies large-scale habitat diversity and its distribution which is ultimately essential for the protection of habitat specific biota. For example, the coastal bathome of northwestern Australia is rich in Level 3 units including deltas, archipelagos, gulfs, lagoons, exposed and sheltered beaches (Lyne et al., 2006). Because these units typically have different biotas, they should be considered independently in the MPA selection process. If any Level 3 unit type is excluded from this process then representativeness of the MPA will be compromised.

Typical units: in coastal bathomes includes fringing reefs, beaches, estuaries, tidal flats, mudflats, drowned river valleys, and marine embayments (Lyne et al., 2006); on continental shelves includes coral cays, glaciation structures, sand banks, deltaic bottoms, and rocky banks (Shepard, 1959; Bax and Williams, 2001; Williams and Bax, 2001; Lyne et al., 2006); and on continental slopes and the abyssal sea floor includes submarine canyons, seamounts, escarpments, plains and valleys (Heap and Harris, 2008) (see Fig. 3C).

3.4. Level 4. Primary biotopes

A biotope has been defined as the smallest geographical unit of the biosphere or of a habitat that can be delimited by convenient boundaries and is characterised by its biota (Lincoln et al., 1998) – they are spatial elements combining the concepts of physical habitat and biological community. Coarsely defined substrate types, sometimes referred to as seascapes or terrains, which are easily identifiable and mappable, and are important determinants of local-scale biological community composition on the sea floor. Entire groups of marine organisms exhibit preferences for either soft or hard substrates (Marshall, 1979) providing an ecologically sound, primary subdivision of benthic habitat.

Geomorphological units were subdivided on the basis of substrate type into soft, hard or mixed substrate-based units, or primary biotopes. Some key biogeophysical processes associated with these units include sediment mobility, availability of infauna habitat, footholds for flora and fauna, retention of biotic resources, and the availability of surfaces for microbial activity and filter feeders. These major abiotic units act as surrogates for assemblages living on or in these substrates. Maps of primary biotopes can generally be obtained from a combination of desktop studies and targeted acoustic surveys to obtain bathymetry, bottom topography, and substrate hardness/softness and roughness. In deep-sea environments, multibeam sonar provides these data at high resolution (Fig. 3D) over areas of 1000s of km^2 (e.g., Kloser et al., 2007) (Fig. 3C).

Biotic structure at this level, represented by habitat at broad spatial scales, is often complex. Key regional features, such as rocky reefs, can be defined by their relief and approximate boundary positions, but cannot serve as surrogates for community structure and composition without adequate ground-truthing. For example, shallow temperate rocky reefs typically have rich assemblages of plants and animals; their substructure at lower levels of the hierarchy (i.e. at facies-level) must be defined to adequately manage their biodiversity. Similarly, different types of soft substrates have different biological assemblages; discrimination between muddy from sandy substrate faunas occurs at the level of secondary biotopes. Levels 4–7 of this framework should be considered as different scales of a biotopic hierarchy.

Typical units include: soft, hard and mixed substrates (see Fig. 3D).

3.5. Level 5. Secondary biotopes

Nested within primary biotopes are smaller-scale, abiotic and/or biotic substructural units of the seafloor characterised by 'specific types' of physical substrate. For example, at this level, the soft substrate primary biotope can be subdivided on particle size to include an array of secondary biotope types such as calcareous ooze, silt, mud and sand. Secondary biotopes that have an associated biological component (e.g., macrobenthos, seagrasses, sponge gardens, mangroves) may be coupled with any of the substrate units above. For example, seagrasses found on muddy and sandy substrates represent separate secondary biotopes because their occurrence is usually substrate dependant and their associated faunal assemblages differ.

Large regional-scale datasets (Levels 1–3) rarely provide useful information at this level. Instead, direct surveys, using benthic sampling equipment or underwater imagery, can be used to obtain geological, biological and ecological information needed for mapping biodiversity at this level and below. However, information on the distribution of secondary biotopes is critical to the selection of small-scale MPAs, and in the planning and monitoring of all MPAs.

Typical units include: igneous, calcareous and sedimentary bedrock, silts, mud, sands, gravels, and seagrass and mangrove stands (see Fig. 3E).

3.6. Level 6. Biological facies

Biological facies are the fundamental units for the management of biodiversity, being firmly nested within all levels above and acting as surrogates for all levels below. They are mappable units characterised by groups or particular species of seagrasses, corals, sponges, or other macro-biotic groups; hence, mobile taxa such as fish are likely to be less informative discriminators of facies than sessile animals and plants. Habitat classification schemes are sometimes schemes for naming and distinguishing facies. Facies are also the extant products of evolution, palaeoclimatic change, and ecological interactions. Their composition and distribution in a particular bioregion is determined by all higher levels of the hierarchy, including hydrological variables such as wave exposure, turbidity, tidal effects and current speed.

In the Australian context, biological facies, considered to be biotopic units (rather than community units or biocoenoses) typically existing as small patches at scales of km or smaller, are identifiable by one or more indicator species that act as surrogates for the broader biological assemblage (or biocoenosis) to which they belong. Biocoenoses, the interacting components of biological or ecological communities within a habitat, are difficult to define and characterise (Stephenson, 1973), so facies act as biological surrogates for biocoenoses by representing a mappable expression of diversity at a community level.

Knowledge of the distribution of facies in a bioregion is important in setting research, management and conservation priorities. Like species, some facies are spatially restricted or rare. These are often most vulnerable to impacts and may need to be given a high conservation priority. The identification of rare and threatened habitat at the facies-level is critical to the MPA selection process where protection of biodiversity is a major outcome. This approach is embodied in Australia's Environmental Protection and Biodiversity Conservation Act where there is provision for listing, according to degree of threat, key facies-level habitat as well as species.

Typical units include: *Macrocystis* (kelp) and *Zostera* (seagrass) stands, and coral communities (see Fig. 3F).

Units below Level 6 are critical for biodiversity management but are generally less relevant for BRMP. Identification and conservation of micro-communities and their component species, populations and genes, will generally be achieved through sustainable management of the higher-level units above. Nevertheless, critical information exists in the micro-scale levels of biodiversity useful for other related purposes, including the management of MPAs and threatened species. It is also essential to understand biodiversity at these scales to capture change and variability in long-term environmental monitoring.

3.7. Level 7. Micro-communities

Micro-communities are herein defined as small-scale assemblages of often highly specialised species that depend on other member species or groups of species within a 'host' facies. In general, adequate protection of facies-level units will ensure conservation of their associated micro-communities. For example, the endofaunal assemblages associated with two sympatric species of sponge of the family Chalinidae (genus *Haliclona*) were found to be significantly different in density and composition (Abdo, 2007). These sponges, which have distinct morphologies and inhabit similar microhabitats, provide important habitats for their associated endofauna. They also have different levels of bioactivity and face very different levels of harvesting pressure. Hence, conservation of the type of facies in which they occur will provide de facto protection for specialist species inhabiting both assemblages.

Other typical units include: endofaunal associations of kelp holdfasts and sponges, and the infauna of muddy sediments.

3.8. Level 8. Species

The species-based units of our hierarchy (Levels 8–10 in our scheme) are the levels of genetic relatedness – of biological diversity in the strict sense. However, they are less important in a biodiversity classification scheme directed at marine planning and management, which typically focuses on Levels 1–6, and in special cases to Level 7. However, lower level units, such as species, are dependent on different higher-level units at different life history stages (i.e. spawning, recruitment, migration and feeding) so the closeness of the link between ecosystem-based and species-based levels of biodiversity should not be underestimated. For completeness of the hierarchy, we briefly discuss these units below in a conservation management context but, as they have been extensively treated elsewhere, these treatments are not intended to be comprehensive.

Biological species are considered to be the basic unit of biological classification (Lincoln et al., 1998). Complete prior knowledge of all relevant species and their distributions would be invaluable information in the MPA planning process; however, this is rarely achievable on land, let alone in the sea where our knowledge of alpha-level taxonomy and community composition is often very poor indeed. In a practical sense, biodiversity conservation at regional scales must be planned and implemented at levels above species. The use of surrogacy to capture species diversity, without having to delineate all species beforehand, depends largely on the assumption that all species adhere to one or more facies.

However, habitat surrogates alone cannot replace a detailed knowledge of species and their life histories. Threatened and endangered species cannot always be managed by habitat protection alone (e.g. whales, tuna, white sharks), as they may move between habitats and even between large-scale regions during their life-cycle. Similarly, fisheries managers cannot adopt a universal approach to the management of marine species with differences in their habitat requirements and life histories. A well-designed network of MPAs and other marine planning and management measures should take account of these circumstances.

Typical units include: species-level taxa, operational taxonomic units (OTUs) and evolutionary significant units (ESUs).

3.9. Level 9. Populations

Populations (and metapopulations) are attributes of species and the way they function and two disjunct populations of the same species usually differ genetically. There is an increasing body of evidence that local biodiversity, and the persistence and coexistence of species, is strongly determined by metapopulation dynamics (Andrewartha and Birch, 1984; Hanski, 1999; Holyoak et al., 2005; Kritzer and Sale, 2006). In marine applications, knowledge of population (or subspecies) structure and dynamics has been mostly applied to fisheries management, but it is increasingly being applied in conservation management. However, because of the complexity and cost involved in understanding population dynamics, it will not be achievable universally for many species and cannot form the basis of BRMP and MPA design in the short term. Populations of micro-endemic species can be identified and protected under the umbrella of province (Level 1) units. Wide-ranging taxa, transgressing multiple provinces within a specific habitat, will obtain de facto protection if conservation measures capture that habitat in each of the provinces in which they occur.

Typical units include: subspecies, phenotypes, and monospecific assemblages of geographic and extralimital isolates.

3.10. Level 10. Genes

Biological diversity at the molecular level is complex and, as much of it is either unknown or hidden from our view, or both, it is necessary to establish means of addressing its distinct and measurable parts (Anon, 1991) – the most basic concept of these is genetic variation (e.g., Noss, 1990; Anon, 1992). Genetic diversity, itself a hierarchical concept, given differing rates of evolution in different parts of the genome, is an important base-line level in our hierarchy. For some kinds of organisms it has been rarely investigated; for others (e.g., microbes) it may be the only way to study their diversity. Genetic variability within and between populations of species affects their physical characteristics, viability, productivity, resilience to stress, and adaptability to change (Anon, 1991). With rare exceptions, this level will not be used in BMP and MPA design, but it may sometimes be important in conservation management of particular species, fisheries management and investigating connectivity between populations.

Typical units include: alleles and DNA sequences.

4. Discussion

Our model of marine biodiversity characterisation expands on existing hierarchical approaches by providing a wider application and larger-scale spatial focus. Extremes of spatial scale and species richness, habitat units varying in size from continents to facies, poor taxonomic knowledge of the biota, and minimal exploration of the seabed, all point to the need for a top-down, rather than a bottom-up, approach to classifying and managing marine biodiversity. Biodiversity surrogate selection is critical to this process but the relevance of different surrogates varies greatly between levels of the hierarchy. Inappropriate selection and use of surrogates can lead to management decisions that fail to address vital aspects of biodiversity (Williams et al., 2009). For example, geophysical surrogates are uninformative at the province level because biogeographic provinces are a product of palaeo-evolutionary history modified by contemporary physical environments (e.g., Ricklefs and Schluter, 1993). Physical surrogates can be used to model extant environments but using them to provide the evolutionary history of even well-known taxa is well beyond our current knowledge and capability. Developments in phylogeography, using molecular clocks and plate tectonics, may provide new insights. Meanwhile, we are constrained to using a combination of biogeographically informative taxa and surrogates to define higher, province-level structure.

Geographically restricted, micro-endemic species are typically more informative for determining fine-scale, biogeographic structure than widespread and ubiquitous taxa. In the Australian model, fishes were used as surrogates for the whole biota because they are relatively data rich (mature taxonomy, species-rich, and with well documented distributions) and have been proven to be indicative of patterns of distribution and evolution and at large (meso) biogeographic scales (Last et al., 2005). Some genera demonstrate high levels of intraregional sibling speciation; their sister species have shared distributions with other unrelated genera providing evidence of province-level structure in the fauna. In comparison, less informative, wide-ranging pelagic fishes, such as tunas (Scombridae), are less useful indicators of mesoscale patterns of evolution. Identifying informative taxa is critical to this process but these groups must have independent evolutionary histories. Ancestral elements of most fish groups used in Australian bioregionalisations are thought to have existed since the fragmentation of Gondwana (ca 85 mya), so the extant fauna is a product of more recent co-evolution. Invertebrate taxa that are rich in endemics, typically those with poorly dispersing or short larval phases, would have been equally informative had their data coverage been more comprehensive. Recent studies using invertebrate taxa have provided supporting evidence for patterns determined by the analyses of fishes (Hooper and Ekins, 2005; O'Hara, 2008a,b; Williams et al., 2010).

The characterisation of provincial (Level 1) and bathomic (Level 2) structure is a critical first step in biodiversity delineation at continental-scales. The importance of using large-scale biogeographic structure, based on evolutionary history to subdivide regions into smaller, more manageable units, is clearly demonstrated with the following example. The temperate seagrass, *Posidonia australis,* is thought to occur widely from central Western Australia to central eastern Australia (Edgar, 1997). In this scenario, inclusion in a MPA at any single location throughout its range will ensure representation of the seagrass; however, conservation of species dependent on this seagrass cannot be guaranteed using this approach. Five distinct, shallow faunal provinces, each represented by unique assemblages of micro-endemic fishes, have been identified off southern Australia (Anon, 1996a; IMCRA (1998)). Species compositions of fish communities in *Posidonia* seagrass habitats differ between each of these bioregions, although the generic compositions are similar between regions. Consequently, the biodiversity of Australian seagrass fishes could not be conserved without firstly, identifying province-level diversity across the region, and secondly, providing protection to seagrass communities in each of these provinces.

Similarly, bathomic regionalisation must be based on biotic rather than abiotic surrogates. Physical data can be modeled to explain patterns in the biota at lower hierarchical levels but cannot be used reliably to predict bathomic structure. However, once the biological data have identified the depth-related structure of bathomes, then these depth intervals can act as surrogates. Mapped bathymetry effectively depicts the distribution of the bathome. Roff and Taylor (2000) flagged the connection between light and depth in controlling what we define as inshore bathomes. Clearly, bathymetric partitioning of species between the infralittoral and deep circalittoral zones is dependent primarily on levels of light penetration. However, community structure on the continental shelf and slope can be equally complex. For example, at least three demersal bathomes exist on the continental shelf off northwestern Australian shelf (Lyne et al., 2006), with four additional bathomes on the adjacent slope (Last et al., 2005). Non-representation of any of these bathomes for BRMP could result in the serious omission of potentially vulnerable stenobathic species from MPA protection or other management measures.

Physical surrogates are essential for characterising geomorphological (Level 3) and biotopic structure (Levels 4 and 5). Rarely are these units biotic in origin, although some variable scale geomorphological units, such as coral atolls and fringing reefs, are combined geological and biological constructs. While biotopes are based largely on geological features, their associated biodiversity is conditional upon units in the levels above.

Unlike most other approaches, our framework consciously focuses on characterising marine biodiversity rather than considering associated biological processes. We acknowledge that both are important in managing biodiversity, but gaining an understanding of processes controlling communities and ecosystems is a difficult task made simpler with prior understanding of its structural complexity. Regional characterisation of biodiversity is simply an initial step in this process. If we had comprehensive regional maps at the facies-level (Level 6) and above, the task of selecting and positioning MPAs to conserve biodiversity would be relatively simple. While small-scale habitat units, such as facies and micro-communities, are partially anthropomorphic representations or surrogates of 'real' communities or biocoenoses, the advantages of managing a spatially represented (i.e. mappable) entity rather than a largely undecipherable construct, should be obvious.

Our hierarchical framework has been used successfully in the Australian context for marine bioregionalisation and has been adopted to guide Australia's BRMP process. However, the greatest source of confusion with this approach has been a failure to recognise the need for strict nesting of levels of the hierarchy. This approach attempts to encapsulate biodiversity variability within levels, with lower levels nested naturally within levels above. However, the approach fails when the hierarchical nature of levels is ignored; jumping erratically between levels can result in the inadvertent omission of elements of the biota. This is clearly demonstrated by an example using submarine canyons (Williams et al., 2009). These canyons can be very large geomorphological features (Level 3), often similar in size or larger in area than their associated bathomes (Level 2). Which is nested in which? Canyons can be viewed as a functional unit of marine ecosystems, unified by certain physical processes (e.g., upwelling, downwelling), but with multiple bathomes each represented by separate canyon-dwelling assemblages. Alternatively, in the context of our approach, bathomes crossing a canyon each contain unique bathymetrically stratified assemblages, subsets of which are smaller assemblages confined largely to the canyon. On face value, the nesting of a larger spatial unit within a smaller one seems unnatural but there are two main advantages of retaining strict nesting of hierarchical levels. Firstly, nesting bathomes (a large-scale, continuous construct) within geomorphological units (medium–large-scale, non-continuous construct) becomes unworkable when the scale of latter is small. Secondly, in a practical sense, candidate canyons can be compared for their biological complexity and regional representiveness based on their bathomic diversity. For example, the biota of a large canyon that extends down most of the continental slope (i.e., across all bathomic intervals) will usually be more representative of the canyon fauna of a province than a small canyon with a narrow depth coverage (i.e., transected by only a few bathomes). Inclusion of a canyon or cluster of canyons in an MPA without all available bathomes being represented is likely to result in the omission of unique elements of its biodiversity.

Wider use of our hierarchical framework as a tool for managing biodiversity is limited by regional data availability and comprehensiveness. Bioregionalisations developed within this framework will continuously need to be refined as marine data gaps are filled. Filling knowledge gaps can be costly so efforts need to be prioritised to most effectively iterate the process. The framework approach assists in making decisions and setting priorities. It also acts as a tool for identifying rare and vulnerable habitat, which can then be subjected to more focused research to evaluate important functional aspects and connectivity, and rare facies can be mapped and contextualized to assist management strategy evaluation. For example, Edgar et al. (2007) used this approach to rapidly scope unique estuarine habitats represented at Port Davey and Bathurst Harbour, southwestern Tasmania, and based on this research parts of the region have now been gazetted as a marine reserve.

A long-term strategic, regional or national-scale approach is needed both to build a better understanding of global-scale marine biodiversity and to pinpoint its key features. Initial application of this framework will help facilitate this objective by capturing the key regional features of biotas relatively simply and cost effectively. The desired endpoints of this process should be to eventually obtain comprehensive, facies-level maps of marine jurisdictions to assist with MPA design and management. However, even in the absence of such detailed information, this framework will provide conservative guidance on the MPA process, particularly for developing nations where facies-level mapping is not presently possible.

5. Conclusions

A 10-level hierarchical framework designed specifically to classify marine biodiversity was developed and applied to assist in understanding and conserving Australia's marine benthic biodiversity by improving on existing definitions which are limited in one or more areas, such as spatial relevance, flexibility, context sensitivity, and surrogacy. Uppermost levels of the hierarchy (provinces and bathomes, Levels 1 and 2) are products of palaeohistorical and evolutionary processes and cannot be determined from abiotic surrogates; geophysical surrogacy is introduced at the next levels down (Levels 3–5). Surrogacy is achieved partly by using a strict nesting approach, and by using constraints imposed by contemporaneous abiotic processes that differentiate habitats. Conservation planners would ideally use finer scale, facies-level maps (Level 6) to identify regions of greatest interest, but as this information is presently unavailable, biodiversity must first be scoped at higher levels of the hierarchy. Our framework provides practical guidance in the use of physical surrogates at appropriate levels in the hierarchy, but they must be ground-truthed in order to provide targeted protection at species or community levels. While management of species or other biodiversity units below the facies-level may be desirable (e.g., threatened and endangered species), for practical management, protection of facies-level units will generally offer defacto protection to units below that level. Our approach differs from existing hierarchical definitions which have a narrower focus, cover a smaller spectrum of biodiversity, and differ in their approach to surrogacy. Our model has been applied successfully in an Australian context at various scales, and a variety of national and Regional Marine Planning projects have been guided and management strategies implemented based on this framework. The approach has potential for broader global application for defining and characterising marine biodiversity.

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