

Narrow range endemism in the sea and its implications for conservation

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ABSTRACT

There is a general, although unfounded, belief that marine organisms are widespread with a low risk of extinction. In reality, many are restricted to small areas with greatly restricted ranges. Narrow range endemics are the result of a combination of intrinsic (biological) and extrinsic (environmental) factors. The latter include history and geography while poor dispersal capability is typically important amongst the former. Oceanic islands, seamounts and specialised deep-sea habitats, such as hot vents and cold seeps, often have significant numbers of narrow-range taxa. Low levels of narrow range endemism can also occur in continental habitats such as estuaries, widely separated intertidal habitats and off-shore islands, reefs and shoals. The conservation of narrow range taxa is of particular concern because these organisms are susceptible to exploitation and habitat degradation.

Key words: endemic species; seamounts; specialised habitats; marine environment; isolation; conservation.

Introduction

While terrestrial conservation has been the main preoccupation of conservation agencies and NGOs, it is becoming increasingly understood there are significant problems in the marine environment, particularly in the coastal zone (e.g. Edgar *et al.* 1991; Norse 1993; Jones and Kaly 1995; Suchanek 1994; Gray 1997; Ponder *et al.* 2002). While the need for conservation of large marine mammals (e.g. whales, seals, dugongs), turtles and some seabirds has long been recognised, there has been only slow recognition that the ocean is not an unlimited resource and that much of it is polluted to some degree. Most commercial marine species are threatened by over-fishing and most of the continental shelf has been severely altered by trawling. Many inshore areas continue to be impacted by development or pollution and few coral reefs are pristine.

The view that most marine animals are widely distributed because of effective means of dispersal by swimming adults or larvae is far from being a universal truth although this view has contributed to the belief that marine species are less prone to extinction than terrestrial species. Lower extinction rates in the marine environment compared with non-marine habitats is also indicated in the available evidence on both modern and fossil extinction rates (e.g., McKinney 1998). Few modern extinctions of marine organisms have been recorded (Carlton 1993; Carlton *et al.* 1999; see examples below) and of these, only a handful are invertebrates¹ or algae and none are minute organisms, such as protists or the vast array of planktonic organisms. This paucity of authenticated cases is almost certainly due to our abysmal lack of knowledge regarding the vast majority of marine life (Ponder *et al.* 2002) and the great difficulty of confirming extinctions in the case of

medium to small-sized organisms, let alone microscopic ones. This paucity of evidence has not, however, deterred warnings about serious impending extinctions of marine organisms (e.g., Malakoff 1997; Roberts and Hawkins 1999; Carlton *et al.* 1999). As with non-marine taxa, marine species occupying very small ranges, usually referred to as narrow ranges, are especially vulnerable to over exploitation and habitat degradation. Yet these taxa receive little attention in debates on marine conservation.

Recent extinctions of species in the marine environment

Proving extinction in terrestrial and freshwater habitats is difficult enough, but these difficulties are increased considerably in the marine environment. A few marine vertebrates are extinct, none of which were widely distributed. These include at least five (Carlton *et al.* 1999) seabirds, all of which had restricted ranges. Of the mammals, Steller's Sea Cow *Hydrodamalis gigas*, occurred only around Bering Island and nearby Copper Island in the Bering Strait, the Caribbean Monk Seal *Monachus tropicalis* previously known from Florida, Puerto Rico and Virgin Islands and the Sea Otter (or Sea Mink) *Mustela macrodon* from the NE coast of North America have been listed as extinct (Vermeij 1993; Carlton *et al.* 1999; Dulvy *et al.* 2002). In addition, extinctions of marine fishes restricted to islands or small groups of islands may have occurred – for example the Green Wrasse *Anampses viridis* from Mauritius, and the Reunion Angelfish *Apolemichthys guezei*, are both probably extinct, as is the Galapagos damsel fish *Azurina eupalama* (Dulvy *et al.* 2002).

¹ The unsatisfactory term invertebrate is used here with some reluctance (see Lunney and Ponder 1999 for discussion). Invertebrates are not a group, comprising many large unrelated phyla of animals, and even some of the Phylum Chordata which includes the relatively small group known as vertebrates.

Because most non-vertebrate marine groups are poorly collected and investigated, there are very few documented extinctions. The only marine invertebrates that have been listed as extinct by IUCN (2002) are the Eelgrass Limpet *Lottia alveus alveus* (Carlton *et al.* 1991; Carlton *et al.* 1999) from eastern North America and a mangrove periwinkle *Littoraria flammea* from China. *Lottia alveus alveus*, previously a rather widely distributed taxon, was associated with *Zostera marina*, which suffered mass mortality in the early 1930s. The *Zostera* survived in brackish water and eventually recovered outside these refugia, but when it did, the limpet, which did not live in brackish habitats, had gone. Another gastropod, the South African limpet *Siphonaria compressa*, lives on *Zostera capensis* and is found in only a single lagoon (Herbert 1999). Clark (1994; 1995) suggested that opisthobranch slugs in Florida were threatened with extinction by the destruction of seagrass and associated epiphytic algae. Several other molluscs, including the chiton *Stenochiton longicymba* and other invertebrates (O'Hara 2002), including the polychaete *Nereis posidoniae* (Hutchings and Rainer 1979), are also restricted to blades of seagrass. *Littoraria flammea* is only known from material collected more than 100 years ago in China (Reid 1986). Other members of this genus are associated with mangroves so it is assumed that this was the habitat of this species. Another reported extinction (Carlton 1993; Carlton *et al.* 1999) is the gastropod *Cerithidea fuscata*, an estuarine snail from San Diego Bay, California, while a closely related and more widespread west coast species, *C. californica*, is displaced from much of its normal habitat by two introduced gastropods (Carlton *et al.* 1999). However, reporting extinctions is a risky business. A NE Pacific endemic "*Collisella*" *edmitchelli*, a rocky shore limpet, was reported as recently extinct (Carlton 1993; Carlton *et al.* 1999) but is actually a Pleistocene extinction (D. Lindberg pers. comm.). Other possibly extinct taxa, the cnidarians *Edwardsia iwella*, an anemone, from the UK and a scleractinian coral *Siderastrea glymi* from the E. Pacific also had small ranges (Dulvy *et al.* 2002). In addition, an alga (*Vanvoorstia benmettiana*) restricted to Sydney Harbour, is now extinct (Millar in press).

The White Abalone *Haliotis sorenseni*, which is now close to extinction due to overexploitation, occurred commonly along the western American coast from Point Conception, California, to Punta Eugenia, Baja California, a linear distance of about 900 km (Tegner *et al.* 1996; Davis *et al.* 1998; Rogers-Bennett *et al.* 2002). Thus, while larger ranges do not necessarily guarantee survival, given the documented examples of extinction, the risk is increased by having a small range.

Narrow range endemism in the marine environment

An endemic (or indigenous) species is one confined to a particular region. A species with a highly constricted geographic distribution, or narrow range endemic in contemporary conservation terms, is, almost *de facto*, a species at risk in a world where the natural environment is degrading. While narrow range endemism is becoming

well recognised for terrestrial and freshwater faunas (e.g., Harvey 2002; Ponder and Colgan 2002), marine animals are generally thought to occupy wide ranges. The terms 'narrow' and 'wide' when applied to the distribution of taxa are relative. Marine temperate biota is often restricted; that of New Zealand is highly endemic, as is the temperate Australian fauna (Poore 1995) and algae (Phillips 2001). There are similar high levels of endemism in southern Africa and America. Similarly, such isolated seas as the Mediterranean Sea and Red Sea have many endemics. This paper is concerned with marine endemism on a much smaller scale – species with distributions less than a few hundred kilometres, or even less than a few tens of kilometres. There are spectacular examples of narrow range endemism in marine organisms, particularly among the invertebrates, although some marine fishes also have narrow ranges.

Species that occupy small ranges are of particular conservation concern if they are exploited or their habitats are degraded or threatened. For example, Musick *et al.* (2000) recognized 82 species, subspecies and Distinct Population Segments (DPSs)² of marine fishes that are vulnerable to extirpation in North American waters. Twelve of these were listed as endemic, or with a small range, with 10 of the 12 considered to be vulnerable to global extinction. Pogonoski *et al.* (2002) identified 114 species of threatened, and potentially threatened, Australian marine and estuarine fishes of the 4100 species recognised from Australian waters. Of these, 35 are confined to a single state, including four of the nine species in the two highest risk categories. However, overall, there are very few fishes with very small ranges – this phenomenon is more typical of invertebrates.

If the thesis that an increase in vulnerability may be positively correlated with a decrease in range size is accepted, is this significant in terms of continental marine faunas? O'Hara and Poore (2000) analysed the ranges of decapod crustaceans and echinoderms in temperate Australia. They examined only species that do not have a wide tropical range and found that 35 (8%) of the 435 temperate species were restricted to a single, one degree cell. Temperate Australia has high species richness compared with many other temperate regions. For example, in south-east Australia (Poore and Wilson 1993; Coleman *et al.* 1997) found 800 species in a few square metres in Bass Strait and 700 in Port Phillip Bay sediments. Thus, if the figure of 8% of the fauna could be used as an approximation of the proportion of restricted taxa across all groups in temperate Australia, the number of narrow range species could be considerable. However, many marine species are only encountered infrequently. In some cases this is because they are rare³ (see Chapman 1999), or live in inaccessible habitats. A more common reason is that very few observations or collections are being made due to the lack of appropriate sampling and the lack of expertise or interest in many groups. Thus it is difficult to accurately delineate the ranges of many marine species with reasonable certainty, or even discriminate the species involved. For this reason, there is bias in the examples given here towards the better-known groups.

² "Distinct Population Segments" (DPS) are defined by the U.S. Fish and Wildlife Service and National Marine Fisheries Service as populations markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors and that are significant to the species to which it belongs. ³ Someone once said that "All species are rare, except where they are common".

Some factors leading to narrow ranges in the marine environment

A combination of, and the interplay between, intrinsic (biological) and extrinsic (environmental) factors determine whether a species will have a narrow range (Ponder and Colgan 2002). In the latter category, historical and geographic factors are important in speciation, as illustrated in crustaceans on a large scale (Newman 1991).

The view that most marine animals are widely distributed because of effective means of dispersal by swimming adults or larvae is not a universal truth. It is true that some are effective dispersers with wide ranges (e.g. much of the Indo-west Pacific). However, those apparently capable of efficient dispersal often show considerable genetic structuring (e.g., Williams and Benzie 1997, 1998; Benzie and Williams 1997; Palumbi *et al.* 1997; Benzie 2000; Lessios *et al.* 2001; Bastidas *et al.* 2001; Triantafillos and Adams 2001; Uthicke and Benzie 2001; Planes and Fauvelot 2002). Distribution patterns largely reflect the success of larval dispersal which may be the result of biological factors other than simply the swimming ability of the larva, as well as the physical properties of the water column, such as currents and water temperature (e.g., Sammarco and Andrews 1988; Gaylord and Gaines 2000). Feeding larvae are probably more effective dispersers because of their ability to maintain a longer larval life. Many others have non-feeding (lecithotrophic) larvae and can show marked genetic structuring (e.g., Parsons 1996; Borsa and Benzie 1996; Forbes *et al.* 1999; Uthicke and Benzie 2000). Others have short larval periods or are direct developers, with brooded young, or with young developing in capsules, as with many gastropods. It is these latter taxa that are typically poor dispersers with high levels of genetic structuring over short distances (e.g., Piertney and Carvalho 1994; Parsons 1996; Carvalho and Piertney 1997; Hoskin 2000; Sponer and Roy 2002; Bastidas *et al.* 2002). These generalisations, reinforced by genetic studies on related intertidal taxa, show that those with larvae that spend time in the water column have less genetic structuring than their relatives with direct development (e.g., Ayre and Hughes 2000; Kyle and Boulding 2000; Wilke and Davis 2000; Collin 2001) or a short larval life (e.g., Parsons 1996; Riginos and Victor 2001). The observation that genetic structuring is commonly seen even within taxa with motile larvae reinforces the idea that speciation is occurring allopatrically in isolated areas, such as the tropical Indo-Pacific (e.g. Palumbi 1992, 1994).

Direct development is often associated with low fecundity and a small geographic range. Range size may also be linked to whether reproduction is predominantly sexual or asexual. In ascidians with obligate sexual reproduction, gene flow is maintained by larvae, while those species relying on asexual reproduction have more highly differentiated local populations (Ayre 1990; Ayre *et al.* 1997). There are many exceptions to this pattern because not all direct developers or clonal organisms have narrow ranges. Minute benthic taxa can be distributed by rafting (e.g., Jackson 1986) or, for short distances at least, in the water column as adults (Martel and Chia 1991). It is conceivable that longer-distance dispersal may occur under

favourable circumstances sufficiently often to maintain genetic continuity. Certainly, based on current taxonomy, some small direct-developing benthic gastropods have wide distributions, with an ability to float being enhanced by the production of mucus strings – a marine analogy of the aerial dispersal of juvenile spiders using silk threads.

Other direct-developers, with large body size, may also have wide distributions if they are highly motile as adults or have available habitat over long distances, such as the continental shelf. In these latter cases, with benthic, sessile or poorly mobile taxa, clinal differentiation will probably occur in conjunction with some genetic substructuring because such extensive habitats are neither uniform nor continuous.

Taxa living in isolated habitats may gain a selective advantage from limited dispersal. Some animals on seamounts have developed strategies for limited dispersal. They gain a selective advantage by retaining the larvae on the seamount, whereas pelagic larvae are likely to be lost in the surrounding ocean (Gofas 1992; Calder 2000).

Specialised habitat and food requirements are additional biological attributes that determine a taxon's distribution. Algal grazers may not only be restricted to certain types of algae, but to those areas and substrates where suitable algae grow (e.g. Clark 1994; Poore *et al.* 2000). Impacts affecting the algae, such as excessive sedimentation, affect the food source, but may not directly affect the herbivore itself. Similarly, carnivores are sometimes highly specialised, often being restricted to a particular group of animals or even a particular species. Commensals and parasites are often highly specific in their host choice. The factors that determine the distribution of the prey or host are the primary factors in the distribution of the predator or commensal or parasite, although other factors may result in these taxa only occupying part of the possible range. Gould (1991) cites the large Bermudan semi-terrestrial hermit crab *Coenobita diogenes*, which is dependent on the shells of a marine whelk *Cittarium pica* that has been fished to extinction in Bermuda. The crab survives only through human intervention – the supply of suitable shells.

Habitat requirements may also differ completely at different stages in the life-history of a species. Specialisation for a particular habitat with limited availability during the development of an organism could result in the geographic restriction of the adult. There are many examples (e.g., Pawlik 1992) of larvae requiring specific types of habitat or chemical stimuli for successful settlement to occur, such influences potentially affecting population size and structure even if there are no obvious factors affecting the adults. Physiological and behavioural attributes are obviously also important in determining the ways in which species interact with their physical environment.

The physical attributes of the environment largely determine the distribution and abundance of marine organisms. Water temperature, currents, salinity, nutrients, oxygen levels, substrate and water depth are vitally important factors and individually or collectively affect the distribution of species. While some effects are subtle, others are dramatic. These factors must also be considered in an historical context.

The linear nature of shorelines and the continental shelf can lead to clinal or allopatric differentiation of taxa through distance or adaptation to changes in the physical or biological characteristics of the environment. The examples given below focus on isolated benthic communities.

Discontinuous habitats. The influence of isolation on genetic continuity depends on the dispersal ability and the degree of isolation. Despite the linear nature of coastlines, coastal habitats are discontinuous. Rocky shores are interspersed with sandy beaches, and estuaries and bays are separated by stretches of open, exposed coast. This lack of continuity does not usually affect the ability of many marine organisms to disperse between suitable patches of habitat within the same biogeographic setting, although it may lead to genetic substructuring, especially in direct developing taxa. Coastlines with large embayments, separated by long stretches of coastline, could lead to local endemism, especially if the coastal configuration is ancient. It is the interplay between current and past configuration that must be considered to understand the present distribution of taxa and the reasons for local endemism. Such consideration must not be confined just to the gross configuration of a shoreline, or to the benthic contours, but to the interaction between discontinuity of habitats and communities and disturbance, both natural and human induced (e.g., Ray 1991, 1996).

Estuaries and coastal lagoons: Embayments, typically estuaries, provide some of the most obvious discontinuities in coastal habitats. Estuarine systems around the Australian coast have been reviewed by Bucher and Saenger (1991). They showed that Queensland has the largest number of estuaries, but it is New South Wales that has most of the threatened estuarine ecosystems.

Hutchings (1999) reviewed the woeful state of the taxonomy of marine invertebrates from Australian estuaries. The four estuaries near Sydney are all different. The best known, and probably the one with the most varied habitats and the largest fauna, is Sydney Harbour. It is also the most modified and polluted. Although the only published list of marine invertebrates was in 1889, we know of about 1200 species of molluscs from Sydney Harbour, which is half the fauna for all of NSW (Australian Museum collection database). A few are known only from Sydney Harbour and may be endemic. Probable endemics, known from Sydney Harbour, include two extinct algae (Miller in press, A. Miller, *pers. comm.*), while the polychaete *Simpliseta limnetica* is restricted to the upper Hawkesbury estuary (Hutchings and Glasby 1982).

Southern Australian estuaries have some well-researched endemics, particularly in south eastern Tasmania. The possibly extinct starfish, *Marginaster littoralis*, has a known range of 1 ha of intertidal zone in the Derwent River estuary (Edgar *et al.* 1991), although the status of this species remains uncertain (Rowland 1996). Another starfish listed as endangered in Tasmania, *Patiriella vivipara*, is found in the same area and is known from only a few localities (Prestedge 1998, 2001). The Spotted Handfish *Brachionichthys hirsutus* is found only in the lower Derwent Estuary and adjoining bays and channels in SE Tasmania⁴.

All three of these taxa have been listed as endangered in Tasmania. Another small starfish found in southeastern Tasmania, *Smilasterias tasmaniae*, was described in 1990 from previously collected material from three localities but surveys in 1994 failed to find the species in the most southerly original localities and it now appears to be restricted to six localities on the western side of Bruny Island where each site probably contains less than 30 animals (Bryant and Jackson 1999). Another brooding species, *Patiriella parvivipara*, is restricted to a few localities near Ceduna in South Australia (O'Hara 2002).

Despite a high species diversity of shallow water invertebrates (Coleman *et al.* 1997), none of the 56 endemics from Victoria, listed by O'Hara (2002, Appendix 1), are confined to embayments. He does, however, note that two rare callinassid shrimps (*Eucalliax tooradin* and *Michelea microphylla*) are known only from Western Port and Port Phillip Bay. One Victorian endemic gastropod, not listed by O'Hara, *Calopia burni*, is found only in Port Phillip Bay, Western Port and Corner Inlet where it lives on seagrass.

The lack of endemism in estuaries is only partly explained by coastal dispersal, especially as some benthic taxa lack swimming larvae. Melville and Burchett (2002) have recently demonstrated genetic differences in the mangrove *Avicennia marina* in Sydney estuaries, but few other studies have been undertaken to seek patterns of genetic structuring in estuarine taxa in Australia. Genetic studies on the estuarine hydrobiid snails *Ascorhis* and *Tatea* show low levels of genetic differentiation between adjacent estuaries. This has been interpreted as reflecting the continuity of those habitats during glacial, low sea levels (Ponder and Clark 1988; Ponder *et al.* 1991).

Coastal intertidal habitats: Coastal, intertidal habitats are rarely continuous over long distances but are interspersed with different substrates, such as rock or sand. Long stretches of unsuitable habitat can provide barriers to dispersal, especially for taxa with limited dispersal capability. Long stretches of sandy coast (e.g., the Gippsland coast) present a dispersal barrier between hard shores, especially for direct developing taxa.

Rock type, including the products of erosion, is important in providing a particular type of substrate and hence microhabitat. Those animals specialised to substrates resulting from particular rock types, will have a distribution that reflects coastal geology. Pebble beaches are uncommon in SE Australia and Tasmania because they depend on infrequent outcrops of hard, fine-grained rock (often basalt). The piles of upper tidal pebbles provide a habitat for a unique assemblage of animals. One of these is *Smeagol*, a genus of small blind slug (Tillier and Ponder 1992). The three named Australian species of these slugs have minute distributions and living in the upper shore their habitats are highly vulnerable to oil spills. Two species are known from the southern coast of Phillip Island, Victoria⁵, the site of two, recent oil spills, one of which is known only from this locality. The other is considered to probably be conspecific with a population in northern Tasmania (Tillier and Ponder 1992).

⁴ <http://ea.gov.au/biodiversity/threatened/information/factsheets/tas2002.html> ⁵ These two taxa were not listed by O'Hara (2002).

Coral reefs: Coral reefs fringe one-sixth of the world's coastlines and are the most biologically diverse of shallow water marine ecosystems (Roberts *et al.* 2002). They are being degraded worldwide by human activities and climate warming, with 58% reported to be threatened by human activities (Bryant *et al.* 1998). Analysis of the geographic ranges of 3235 coral reef species revealed that between 7.2% and 53.6% of each taxon have highly restricted ranges, rendering them vulnerable to extinction (Roberts *et al.* 2002). They showed that restricted-range species are clustered into centres of endemism with the 10 richest (with 44.8 - 54.2% of the restricted-range species) including 15.8% of the world's coral reefs (0.012% of the area occupied by oceans). Many of these endemism hotspots occur in regions where reefs are being severely impacted, potentially leading to many extinctions. The analysis by Roberts *et al.* (2002) was based on only a small fraction of coral reef diversity, as 77.4% of the species considered were fishes and corals, with the remainder comprising only 69 species of rock lobsters and three families of gastropods.

Reaka-Kudla (1997) estimated that there were 93,000 described species living in coral reefs, but that this might represent only 1-15% of the actual number of species. Carlton *et al.* (1999) argued that, if only 5% of the world's reef area has already been severely degraded, then about 1000 (1.3%) of the described reef species may already be extinct. If reef destruction increased to 30% (as often predicted) about 10% of reef species would become extinct. Reaka-Kudla's (1997) estimates on actual numbers of coral reef taxa are supported by some recent findings which demonstrate that the majority of many reef invertebrates are still unnamed. Bouchet (2000) and Bouchet *et al.* (2002) have shown that a small area of coral reef habitat in New Caledonia contained 2781 species of molluscs, many of which are unnamed. Some groups are much more poorly known. Newman and Cannon (1994) documented 134 species of polyclads from the Great Barrier Reef, over 90% of which were new.

The deep-sea: Although once regarded as depauperate, the deep-sea invertebrate fauna is actually highly diverse (Wilson and Hessler 1987; Grassle 1991; Grassle and Maciolek 1992; Rex *et al.* 1993; Blake 1994; Blake and Grassle 1994; Blake and Hilbig 1994; Gage 1996). While deep-sea (>3000 m) benthic macroinvertebrates include species with broad, near cosmopolitan geographical distributions, others have more limited, sometimes local, ranges (Wilson and Hessler 1987; Gage and Tyler 1991). Deep-sea taxa typically have reduced or absent planktonic dispersal. Species restricted in depth, and groups with a high proportion of truly abyssal species, show a high level of endemism, with 95% of hadal (> 6000 m) species occurring only in a single trench or a group of adjacent trenches (Vinogradova 1997). With the dearth of deep-sea sampling in Australian waters, we know virtually nothing about them, although the diversity of the deepwater isopod fauna off south eastern Australia rivals that anywhere else in the world (Poore *et al.* 1994) and this diversity may well be reflected in the as yet-unstudied diversity in other taxa. In stark contrast to the lack of work in Australia, an extensive program in deeper waters surrounding New Caledonia has revealed a rich fauna with apparently high endemism (e.g., Crosnier and Bouchet 1991; Bouchet 1995; Bouchet and Marshall 2001).

Isolated habitats: Oceanic islands, especially those on the fringes of the tropics, tend to have high levels of endemism. The islands do not need to be isolated and those that lie on the edge of the tropics often have a higher level of endemism than those in the tropics (e.g., Briggs 1999). The Houtman Abrolhos, Western Australia, at about 28° S., are only about 50 kms from the mainland but populations of some gastropods on these islands are genetically isolated from those on the mainland (Pudovskis *et al.* 2001). The volute *Amoria macandrewi* is known only from Barrow Island and the nearby Monte Bello Islands, NW Australia (Wilson 1994) which are only about 55 km off the mainland coast.

Lord Howe Island lies at 31°30'S latitude, some 700 km north-east of Sydney and has a mixed tropical and temperate biota. There are 305 species of algae (15% endemic) (Millar and Kraft 1993; 1994a; 1994b), at least 83 species of coral (none endemic) (Harriott *et al.* 1995), more than 65 species of echinoderms (6% endemic) (Pollard and Burchmore 1985) and over 447 species of fish (4% endemic to Lord Howe and Norfolk Islands) (Pollard and Burchmore 1985). A handful of benthic samples taken from less than 40 m depth on the shelf around the island showed relatively high endemism (13.1 per cent to Lord Howe Island) of the rather rich shelf invertebrate fauna, the majority of these endemics (9.8 per cent) being restricted just to the shelf (Ponder *et al.* 2000).

The entire marine fauna of the Galapagos Islands is 33% endemic (Bustamante *et al.* 2000). When all marine biota is considered, Bermuda, 946 km from the nearest land, has only 2.4% endemism while Hawaii has 11.8% (Sterrer 1998). Some groups, such as molluscs tend to have a higher proportion of endemics. For example, 19% of the marine molluscs of the Kermadec Islands are endemic (Brook 1998), as are 20% of those at the Hawaiian Islands and 37% at the isolated Easter Island (Rehder 1980).

Time to accumulate taxa in isolated locations is also critical to acquiring genetic variation and exhibiting differentiation. The isolated Pitcairn Islands are late Tertiary in age (Fosberg *et al.* 1983). Its marine molluscan fauna is impoverished in comparison with those found on islands farther west. It is mainly composed of widespread Indo-West Pacific species, with only a few endemics (Preece 1995). The fishes also show low endemism (Irving *et al.* 1995). Only 4 of the 52 species of echinoderms known from the five million year old Macquarie Island in the southern ocean are endemics (O'Hara 1998), although it has only been emergent (and hence provide a habitat for intertidal and shallow sublittoral species) somewhere between 700,000 and 80,000 years (Roberts 2000). The extremely high levels of endemism on some young islands have been attributed to the previous existence of much older islands – particularly where island chains have formed over mantle hotspots. The Galapagos Islands have a maximum age of 4.5 mya (White *et al.* 1993) but are associated with a chain of much older seamounts (5-11 mya), presumably the remnants of eroded islands (Christie *et al.* 1992). The interpretation was derived from recent molecular evidence for some terrestrial taxa (e.g. Sequeira *et al.* 2000). Similar scenarios have been suggested for other islands with high endemism (e.g. Hawaii and Lord Howe).

Banks, reefs and shoals: Isolated reefs, shoals and submarine banks often contain endemics. They are typically the eroded remnants of islands, so they can be expected to have had more time than young islands to acquire endemics. Nearly 4% of the species of molluscs and echinoderms on Middleton and Elizabeth Reefs east of Australia are endemic to them and nearby Lord Howe and Norfolk Islands (Hutchings 1992), but the only endemics to the reefs themselves are 1.3% of the molluscs. Allopatric speciation can occur between isolated reefs within the same general area. In the Coral Sea, the volute *Cymbiola perplicata* is restricted to Diamond, Mellish and Lihou Reefs, while *C. thatcheri* is found only on Chesterfield, Bellona and Bampton Reefs (Wilson 1994).

These reefs do not need to be far offshore to show major faunal differences, including the degree of endemism, to mainland habitats. Hooper and Kennedy (2002) noted that up to 57% of sponge species on 10 small reefs and shoals just off the Sunshine Coast, Queensland, were found on only one reef while Hooper *et al.* (1999) showed that Wreck Reef, in the Coral Sea, has 46% endemism in its sponge fauna compared with other eastern Australian locations.

Seamounts: Seamounts are found in many parts of the world. They provide deeper-water habitats than shoals and reefs. They are usually the tops of extinct volcanoes that have eroded and sunk below sea-level to form steep-sided islands of shallow substrate surrounded by deep water. The communities living on the seamounts are often dominated by colonial organisms, such as corals and other filter feeders (Genin *et al.* 1986; Koslow and Gowlett-Holmes 1998). These fascinating habitats have long been neglected, especially those in the Indo-Pacific (Rogers 1994), with only a few recent studies. They typically have endemic taxa associated with them because they are often isolated from other shallow-water areas (Gofas 1992; Koslow and Gowlett-Holmes 1998; Richer de Forges 1993; Richer de Forges *et al.* 2000), although low endemism or even absence of endemism, has been recorded, especially in those seamounts close to continental areas (e.g., Ramil *et al.* 1998; Gillet and Dauvin 2000; Calder 2000).

The number of species of gastropods decreases significantly from the continent towards the easternmost seamounts in a chain off eastern Brazil (Leal and Bouchet 1991), with dispersal, presumably via larvae, across the relatively small distances (100-250 km) that separate the summits in this chain. The gastropod fauna of seamounts near Portugal shows high endemism in small taxa with non-planktotrophic larvae (Gofas 1992). Seamounts are also home to some important relictual taxa. A living-fossil sea lily, *Gymnocrinus richeri*, was discovered on seamounts south of New Caledonia (Ameziane-Cominardi *et al.* 1987; Bourseau *et al.* 1987) and sphinctozoan calcareous sponges, thought to have disappeared about 70 million years ago, were also discovered on these seamounts (Pichon 1995).

Isolated deep-sea habitats: Isolated deep-sea habitats formed by cold seeps and hot vents have highly specialised, often relictual, faunas with high levels of endemism (e.g.,

Jollivet 1996; Peek *et al.* 1997; McArthur and Tunnicliffe 1998; Tunnicliffe *et al.* 1998; Laubier 2001; Fujikura *et al.* 2002). The sea daisy (*Ophiopholis aculeata*) originally described as the sole member of an echinoderm class, Coccinicycloidea⁶, lives only on wood in the deep-sea. A number of other taxa (mainly limpets) are restricted to wood and other deep-sea biogenic substrates such as whale bones and cephalopod beaks (e.g. McLean 1992; Marshall 1987, 1994, 1996; Warén 1996), although some taxa have affinities with those in cold seeps and hot vents (Smith and Baco 1998).

Margins of major biogeographic areas: Areas of endemism around coastlines are the result of a combination of geographic, oceanographic and historical factors. South Western Australia has a number of Tethyan relicts (Wilson and Allen 1987) while the Capricorn Channel at the end of the Great Barrier Reef has apparently relictual endemic gastropods with their closest relatives in the Miocene of Victoria (Darragh 1979).

Overlap zones of major marine "provinces" often contain endemic faunas, some of which occupy narrow ranges. For example, the subtropical area south of the Barrier Reef to northern New South Wales contains a number of endemics, some with short ranges – for example the gastropods *Lryeneta laseroni* and *Fusinus consetti* are known only from northern New South Wales while *Nodopelagia brazieri* extends from Caloundra, Queensland, to the mouth of the Redbank River, northern NSW (Wilson 1994). There are also endemic offshore gastropod taxa in this area including *Athleta studeri*, *Nannamoria parabola*, *Hastellum tweedianum*, *Chicoreous longicornus*, *Bolma aureola* and *Latirus staminatus*.

Isolated basins and inland seas: Large, enclosed areas of sea sometimes contain endemics. The Ariake Inland Sea, Kyushu, Japan, has several endemics, including four molluscs, a fish, and two polychaetes as well as several species otherwise only found on the Chinese and Korean coasts (Sato 2000). Completely enclosed inland seas (e.g. Caspian and Black Seas), have high levels of endemism and are among the most endangered ecosystems in the world, but are beyond the scope of this paper.

Discussion

Most of the examples presented in this paper are based on a few, well-known marine groups (fishes, corals, and some echinoderms, molluscs and sponges) where narrow-range endemism can be convincingly demonstrated. In many instances poor sampling may result in apparent narrow range endemism. Each case can be evaluated on the basis of the intensity of the sampling for the target species, and/or for similar species (e.g., Ponder *et al.* 2001). Restriction and isolation of habitat may provide a convincing *a priori* argument for endemism, but this must be tested with sampling from suitable habitat from surrounding areas before endemism is proven. It can be expected that, with resources to carry out the necessary research, narrow range endemics will be found in most of the major marine taxa. Our lack of knowledge is profound, given (1) previously unsuspected

⁶ Now thought to be an aberrant asteroid.

extraordinarily high species-level diversity in marine ecosystems, (2) basic sampling for most groups of animals is inadequate for many coastal areas and the shelf, let alone the slope and deep-sea, (3) the taxonomic impediment (see Ponder *et al.* 2002) and (4) the undoubted presence of many unrecognised sibling species (Knowlton 1993), even in supposedly well-known groups. This ignorance is matched only by our comparatively small efforts to conserve marine habitats and organisms. The narrow range endemic taxa illustrate the need for broader-scale conservation strategies. It is imperative that we think simultaneously in different scales about how to conserve our marine fauna. This particularly applies to those organisms which, from a policy perspective, are lumped into that amorphous group called the invertebrates (Lunney and Ponder 1999). Some of the issues and ways forward are outlined below.

Conservation issues for narrow range marine taxa

Vulnerability of narrow range marine taxa

Restricted ranges for marine taxa are considered to be important as a threat criterion (e.g., Jones and Kaly 1995; Ponder *et al.* 2002). Using the IUCN threat categories, any taxon with a range of less than 100 km² is considered as vulnerable (IUCN criterion D2). There is a greater chance of extinction, as a result of stochastic events or disturbance, for a taxon with its distribution limited to a small area. Narrow range taxa, by their very nature, typically have either a low capacity for dispersal from an impacted area or specialised habitat preferences that would severely limit their capacity to colonise a new area. Habitat specialisation renders a taxon vulnerable if the habitat itself is threatened, this being the main factor in apparent recent extinctions of marine gastropods (Carlton 1993). Many organisms, such as corals, are currently living near their upper or lower thermal limit (e.g., Hatcher *et al.* 1989) hence there may be little margin for adaptation to environmental change. Taxa occupying only a small area would be particularly vulnerable to even local changes. Thus some narrow range taxa may be at risk because they have a narrow ecological niche, or are living near the limits of their environmental tolerance.

Parasitism and commensalism are strategies that often involve specialisation for a particular “habitat”, i.e. an associate or host species. For example, many trematodes (and others) require intermediate host species or vectors (e.g., snails, birds, fish). Commensals with, or parasites of, locally endemic species, or species with a severely contracted range, would in turn become vulnerable as the host or associate species becomes vulnerable.

Human impacts on coastal and other marine ecosystems

Some human activities resulting in habitat degradation, or other modifications to the marine environment, profoundly affect pelagic and benthic communities alike and have the potential to result in local extinction, and in the case of narrow-range taxa, their complete extermination.

Such impacts include:

- *Trawling and dredging.* By far the most widespread impact is the result of fishing, particularly trawling, or other destructive fishing methods, such as scallop dredging. They destroy the three dimensional structure of benthic communities (e.g., Hutchings 1990; Watling and Norse 1998; Thrush *et al.* 1998, 2001) and consequently most continental shelves and benthic habitats in estuaries and bays are severely modified. Trawling and dredging damage habitats and species other than those directly exploited (e.g., Jones 1992; Morton 1996; Jennings *et al.* 2001; Thrush *et al.* 2001) irrespective of whether they are part of the bycatch. If a damaged habitat is small, and contains narrow range taxa, there is a high potential for extinction. For example, the faunas of seamounts are highly localised and vulnerable to such activities (e.g., Koslow *et al.* 2000; 2001). In seamounts south of Tasmania, the most heavily fished showed significant damage, with 59% fewer species per sample compared with the lightly-fished or unfished seamounts (Koslow and Gowlett-Holmes 1998).
- *Coastal development.* This has resulted in the modification and even complete loss of many coastal environments, with estuarine habitats and the supralittoral zone (e.g., Richardson *et al.* 1997) being among the most impacted. In Japan, the modification of coastlines in bays and estuaries has resulted in a huge reduction in habitat. Of the 465 species of macroinvertebrates identified as being restricted to saltmarsh and estuarine environments, 389 species (83.7%) became designated as threatened with a few probably already extinct (Wada *et al.* 1996).
- *Pollution.* This ranges from oil spills and waste disposal to agricultural runoff and antifouling chemicals. Such pollutants are the norm in much of the world's coastal zones.
- *Introduction of exotics.* Competition or predation by exotic species can cause substantial declines or local extinction, and hundreds of species have now been introduced to marine and estuarine ecosystems around the world (e.g., Pollard and Hutchings 1990; Ruiz *et al.* 1997; Bax *et al.* 2001).
- *Climate change.* Increasing global temperatures are recognised as being a serious threat to coral reefs and other shallow-water habitats (e.g., Hoegh-Guldberg 1999; Ponder *et al.* 2002), as well as the changes to intertidal habitats and coastlines as a result of rising sea levels.

Another category of human impact is direct exploitation. Overfishing was the original, and remains, one of the major impacts of humans on coastal ecosystems (e.g., Jennings and Kaiser 1998; Jackson *et al.* 2001). Narrow range endemics are more susceptible to extinction than wide-ranging taxa if they are directly and unsustainably exploited. Roberts and Hawkins (1999) and Ponder *et al.* (2002) identified the characteristics that render marine taxa vulnerable to extinction. These include those species with small geographic ranges. Other risk factors are high “value” and accessibility. While direct targeting of vertebrate taxa is

extensively documented, other activities, such as the bait industry and the coral and specimen shell trade, target wild populations of invertebrates, yet are not normally regarded as commercial fisheries and consequently have a low profile. Nevertheless, specimen shell harvesting in particular does target many narrow range taxa because these often have a high value among collectors (Ponder and Grayson 1998). Decline in other species of interest to shell collectors are more related to habitat degradation or loss, or to inadvertent capture (“by catch”) in fishing operations. For example, the endemic Australian cowries *Zoila* spp. and *Umbilia* spp. are associated with large cup sponges, a habitat greatly depleted by commercial trawling operations on many parts of the continental shelf (Ponder and Grayson 1998). Similarly, large volutes, some with small ranges, were once common on the S. E. Australian shelf but are now seen only infrequently.

Areas that are inaccessible to fishing trawlers may act as refuges, and theoretically enable recolonisation of the accessible, more heavily exploited habitats. However, such refuges are likely to be different and not necessarily share most of the biota of the exploited area. Further, the number and extent of refuge habitats are diminishing as improvements in technology enable fishing operations to reach previously-inaccessible reefs, deep-sea habitats and seamounts.

Conservation actions

The prevention of extinction requires knowledge – no action will be taken regarding an ecosystem or taxon in crisis if no one knows about it. For most marine taxa, particularly invertebrates, there are little data available and extinctions are probably occurring without being noticed. More use needs to be made of available data as a starting point. While some information is available in the literature, or directly from experts, museum collections can potentially provide the best information on the distribution and habitat preferences of most invertebrates (e.g., Hawksworth and Mound 1991; Mehrhoff 1997; Ponder 1999; Ponder *et al.* 2001), including helping to identify narrow range taxa that may be at risk. These data will provide the necessary background to undertake new survey work directed at significant habitats and/or taxa. Coupled with these more obvious strategies are other, oft-cited needs, such as the training of more taxonomists and the synthesis of available data so that information is readily usable, preferably in a web-based format (Ponder *et al.* 2002).

Listing threatened marine taxa is another conservation strategy which may work well for a small number of relatively high-profile, well researched species but it will

never address the conservation needs of the great bulk of threatened marine taxa (Ponder *et al.* 2002; Hutchings 2003). To date, very few marine taxa are listed under Australian legislation⁷. While there are some papers on the conservation of marine invertebrates in Victoria (e.g. Norman and Sant 1995; O’Hara and Barmby 2000), other Australian states lag far behind.

Unfortunately, the widely-held belief that conserving representative marine ecosystems is a conservation strategy that will cater for all marine biodiversity does not hold true for those narrow-range taxa whose entire range falls outside the protected areas. Given that areas for reserves are often selected by using habitats as surrogates (e.g. Ward *et al.* 1999), often with a bias towards particular habitat types (e.g. Hatcher *et al.* 1989), and usually combined with a healthy dose of political expediency, the chances of low-profile narrow range taxa being incorporated are small.

Narrow range endemics will be particularly vulnerable in a conservation approach that relies on marine protected areas alone until ranking priorities for conservation action includes the identification of those areas important for vulnerable narrow-range endemics across a wide range of taxa. Once these are identified and incorporated in marine protected areas, this strategy will assist with the conservation of these taxa. However, their inclusion in marine protected areas does not guarantee that the habitats essential for a particular taxon will remain unaltered (e.g., Allison *et al.* 1998) given the substantial changes that have been documented in some marine ecosystems over relatively short periods of time (e.g., Wilson *et al.* 1998).

Many of the less conspicuous narrow range taxa highlight organisms in urgent need of attention by committees dedicated to considering future conservation options. They serve to illustrate the fundamental difficulties of conserving all environments, not only those in the marine realm, and thereby expose the current limits in the conceptual framework for conserving biodiversity. Methods employed to determine significant areas for protection, in particular, the widespread use of inappropriate surrogates, must be improved. A useful test to apply to any strategy that claims to conserve biodiversity of a particular area, whether it be a coastline, a catchment, an entire state or territory, or an entire continent, are the questions: “has the available data for a range of taxa (ie. including a number of invertebrate groups!) been examined to determine the extent of narrow range endemism” and “is there a strategy in place to conserve narrow range endemic taxa?” Until that answer is, “yes” to both questions, there is no case for relaxing our conservation endeavours.

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⁷ CSIRO. Action plan for threatened non-marine invertebrates. http://www.ento.csiro.au/conservation/areaof_research/actionplans/action_plan.html (lists all listed Australian threatened invertebrates).

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