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Chapter 8

Corals on seamounts

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Abstract

Corals are amongst the most conspicuous sessile organisms found on the hard substrates of seamounts. They include a diverse array of groups within the phylum Cnidaria, including the Scleractinia (stony corals), Antipatharia (black corals), Zoanthidea (zoanthids), Octocorallia (gorgonians, sea fans, soft corals) and Stylasteridae (hydrocorals). Estimating global coral diversity on seamounts is complicated by a lack of samples. However, they are an important component of the species diversity found on seamounts, playing a pivotal role in structuring the environment. In particular, some scleractinian corals have the ability to form cold-water reefs that may have a diverse community of associated organisms. Gorgonian corals may form dense stands that also play a structural role in communities of fish and other organisms. Corals found on seamounts show a diverse range of life histories although patterns of recruitment to populations are not understood. Isotopic methods for ageing corals have revealed that individual colonies may be slow growing and can live for hundreds to thousands of years. The distribution of corals on seamounts depends on a variety of physical and biological factors. Relative distribution of the coral groups differs regionally and between oceans, reflecting differences in ocean chemistry, productivity and biogeography. The different coral groups also show significant differences in depth of occurrence resulting from differences in trophic ecology and other aspects of biology. Because of their fragility, conservative life histories and limited geographic distribution, cold-water corals are vulnerable to the impacts of human exploitation through coral harvesting or as bycatch of fishing, especially trawling. Changes in ocean chemistry resulting from climate change are also a significant threat to corals on seamounts and other marine habitats.

Introduction

Corals are conspicuous, long-lived residents of seamounts of great interest to marine biologists and conservationists because of the ability of some species to form cold-water reefs. These reefs may be associated with diverse communities of other species that live in the variety of habitats formed by the living and dead framework-building coral (e.g., Freiwald *et al*., 2002). However, the number of coral species that form such complex reef structures is relatively small (Roberts *et al*., 2006). Many species occur as solitary colonies,

are themselves associated with other corals, or may enhance habitat complexity in other ways, for example by forming coral meadows, forests or beds (e.g., Brodeur, 2001). This chapter reviews the current knowledge of the ecology and distribution of corals on seamounts, ridges and banks of the world's oceans. This is achieved through review of existing studies on the biology and ecology of corals on seamounts and by the analysis of 3215 records of corals available in scientific literature, museum records and databases. In this analysis, we have used a broad definition of seamounts (see Preface) as there is no 'typical' seamount feature, and they differ markedly in size, depth, elevation, geological associations, origin, distance to the continental slope and oceanographic setting (Rowden *et al*., 2005; Chapters 1 and 2). Thus, we have included everything from shallow banks, associated with the slope of the continental margins and oceanic islands, to isolated oceanic seamounts. All records used in this analysis are available on Seamounts Online.

Diversity and ecology of corals on seamounts, ridges and banks

Diversity

Corals are all from the phylum Cnidaria. Those that occur on seamounts are mainly from the class Anthozoa and include the hexacorals of the orders Scleractinia (stony corals), Antipatharia (black corals) and Zoanthidea (zoanthids); and the Octocorallia (gorgonians or 'sea fans'). The class Hydrozoa, or hydrocorals, is represented by the family Stylasteridae. Out of the 526 species of corals recorded on seamounts and banks, stony corals are the most diverse and commonly observed group (Table 8.1). This is followed by the octocorals, the stylasterids, the antipatharians and the zoanthids in order of diversity and number of records (Table 8.1). Even when records are considered only from oceanic

Table 8.1 Number of species, genera and families of corals (Scleractinia, Octocorallia, Antipatharia, Zoanthidea, Stylasterida) recorded on seamounts and banks and seamounts only (in parentheses).

Taxonomic category/ taxon	Total number of records	Number of species	Number of genera	Number of families
Scleractinia	1713	249 (165)	85 (61)	20 (14)
Octocorallia	957	161 (110)	68 (49)	21 (17)
Antipatharia	157	34 (24)	22 (17)	6 (6)
Zoanthidea	28	14 (2)	6 (2)	3 (2)
Stylasteridae	372	68 (53)	18 (17)	2 (2)

seamounts, excluding banks connected to the slopes of continents and islands, there are still 354 species recorded. Comparisons with records held in 'Seamounts Online' show that more species of corals (Cnidaria) have been recorded from seamounts than any other group of invertebrates (Stocks, 2004). The species diversity of corals on seamounts and banks is similar to that of fishes found on seamounts, although the latter represent a larger number of families (130 in fish; Froese and Sampang, 2004). The species richness of corals on seamounts shows that the megafauna of these habitats are predominately

sessile, filter-feeding organisms (Rogers, 1994; Stocks, 2004). This is because of the nature of seabed and the vigorous hydrodynamic regime on seamounts compared to most other deep-sea habitats (see Chapters 4 and 7).

Approximately 1482 species of scleractinian corals have been described of which more than half (about 800) are associated with shallow tropical reefs (Paulay, 1996), and about 706 are azooxanthellate, which lack symbiotic algae (S.D. Cairns, Smithsonian Institution, Personal communication, 2005). Of the azooxanthellate species, about 615 have been recorded from depths greater than 50 m. Seamounts and banks therefore potentially host a substantial fraction of the global scleractinian fauna and a very large fraction of azoox-anthellate species. Many of the zooxanthellate species, genera and even families, common on shallow-water reefs (Paulay, 1996), are eliminated from the seamount fauna if island and continental slope-associated banks are excluded from this dataset (e.g., families Acroporidae, Meandrinidae Mussidae; genus *Agaricia*). This is because many of these topographic features have shallow summits, suitable for formation of warm-water reefs.

Over 2700 species of octocorals have been described (Freiwald *et al*., 2004) of which about 6% have been recorded from seamounts and banks. This does not reflect the importance of this group either in terms of species diversity or of abundance as components of the seamount fauna. The antipatharians and zoanthids are less well known. The Zoanthidea in particular are poorly represented in this dataset. This is because the taxonomy of these groups is very poorly understood and many zoanthids species are very small and difficult to observe or sample.

Factors determining the distribution of corals on seamounts

Seamounts act as biological hotspots in the oceans and often attract a high abundance and diversity of large predators such as sharks, tuna, billfish, turtles, seabirds and marine mammals (Chapter 12; Worm *et al*., 2003; Dower and Brodeur, 2004; Yen *et al*., 2004; Tynan *et al*., 2005). In the food-stressed environment of oligotrophic oceans, these features may be critical for the survival of many pelagic species. Seamounts can also host diverse and abundant communities of benthic organisms dominated by suspension feeders, including corals, sea anemones, sea pens, hydroids, sponges and feather stars (Rogers, 1994; Stocks, 2004). These communities differ from those found on the sediment-covered continental slopes and abyssal plains that are dominated by deposit feeding organisms such as holothurians (Gage and Tyler, 1991).

Rogers (1994) suggests two main explanations why seamounts host such diverse benthic and pelagic communities. These are increased productivity resulting from upwelling of nutrient-rich deep seawater around seamounts (Chapter 4) or the trapping of layers of diurnally migrating zooplankton, advected over seamount summits at night (Chapter 5). Increased productivity over seamounts and other elevated topography requires that upwelled, nutrient-rich water is resident over the feature for sufficiently long to enhance phytoplankton growth and for this to be converted to increased populations of zooplankton grazers (see Chapter 4).

Evidence of increased primary productivity over seamounts is rare and hard to connect to increased populations of benthic organisms (Genin, 2004). The topographic trapping of descending layers of zooplankton has been observed as providing a source of food for

seamount-associated species in several cases (e.g., Genin *et al.*, 1988; Seki and Somerton, 1994; Parin *et al.*, 1997; Haury *et al.*, 2000; Chapter 5). Whether or not this takes place depends on the depth of the seamount summit, with respect to the depths over which the deep scattering layers (DSLs) of plankton migrate, and the intensity of horizontal currents that advect the DSL over the seamount at night (Genin, 2004). This would appear to be an important mechanism of trophic focusing over many seamounts (Rogers, 1994; Genin, 2004). Evidence that seamount corals prey on the DSL is lacking although *Lophelia pertusa* has been observed to prey on planktonic copepods (Freiwald, 1998). Analyses of the ^{15}N and ^{13}C isotope signatures of the tissues of *L. pertusa*, from the Galicia Bank, NE Atlantic, are also consistent with a diet that comprises a significant proportion of zooplankton (Duineveld *et al.*, 2004). Analysis of the distribution of stony corals and stylasterids (see below) shows that the majority of species occur in the depth range 100–1000 m. This depth distribution is consistent with trapping of the DSL and the availability of prey from this food source may be a determining factor in broad-scale patterns of distribution of stony corals on seamounts. Gorgonians and antipatharian corals have a greater tendency to be distributed below 1200 m (see later and also Etnoyer and Morgan, 2005). Octocorals have a relatively low density and diversity of nematocysts (Mariscal and Bigger, 1977) and, unlike stony corals such as *L. pertusa* that can feed on active zooplankton such as copepods, tend to be passive suspension feeders that capture prey items with little or no ability to escape (Ribes *et al.*, 2003). They can also exploit food sources such as particulate organic matter and microbial eukaryotes (Ribes *et al.*, 2003). This may allow them to exploit food sources unavailable to stony corals and stylasterids at abyssal depths. These sources may include micro- or nanozooplankton and dead organic particulate material flowing past or raining down on the seamount and material resuspended from the seabed as a result of accelerated or turbulent current flows. Little is understood about the energetics of deep-sea corals and it may also be the case that food concentration and quality are insufficient at greater depths for many species of scleractinians and stylasterids.

Studies on individual seamounts have demonstrated the strong influence of current strength on the distribution of corals. Current strength may be positively correlated with food supply and negatively correlated with sediment cover on seamounts. Corals require hard substrates for attachment, including bedrock, cobbles, stones and even the skeletons of other corals, the tubes of worms or the shells of marine molluscs. Currents keep feeding structures clear of sediment, remove waste products and disperse gametes or eggs and larvae (Grigg, 1974, 1984). Observations on Pacific seamounts have shown that at large scales, gorgonians and antipatharian corals are abundant near the peaks of seamounts, especially around the rims of summits or near the edges of terraces or basalt dykes where currents are strongest (Genin *et al.*, 1986; Moskalev and Galkin, 1986; Grigg *et al.*, 1987; Matsumoto, 2005). On smaller scales, densities of *Stichopathes* spp. have been observed to increase on rock pinnacles (Genin *et al.*, 1986). Strong negative correlations in coral abundance with sediment cover have also been observed on seamounts (Genin *et al.*, 1986; Grigg *et al.*, 1987).

Studies on Great Meteor Seamount in the Atlantic have shown differences of two orders of magnitude in the abundance of corals on the peaks of the seamount compared to the slopes (Piepenberg and Müller, 2004). This distribution was consistent with strong currents over the seamount. However, even on the seamount summit, the

occurrence of corals was very patchy and this was attributable to the presence of sediments and the occurrence of turbulent flow. The effects of turbulence on food supply for corals on seamounts has not been investigated, although the complex tree-like branched form of many species found on seamounts can be viewed as advantageous for feeding in a regime where currents may frequently change direction and strength. Turbulence may also influence patterns of larval settlement over small scales.

Observations of the distribution of the coral *L. pertusa* in non-seamount and seamount habitats also show that this coral is found in areas of strong current flow (Rogers, 1999). On Cobb Seamount, in the NE Pacific, this coral occurs in areas of strong unidirectional flow (Farrow and Durant, 1985), whilst on the Rockall Bank it occurs around the summit 'rim' and on smaller scales, tends to grow on the mounds formed by the edges of old iceberg furrows called levees (Wilson, 1979a). Iceberg furrows have a particularly strong influence on the structure of the large *L. pertusa* reef on the Sula Ridge in the NE Atlantic (Freiwald, 1998).

Reproduction and life histories

There is no specific published information to date on reproduction of corals from seamount habitats, although studies have been carried out on deep-sea corals some of which occur on seamounts and banks (Waller *et al*., 2002, 2005; Waller, 2005; Waller and Baco-Taylor, 2005; Waller and Tyler, 2005). Corals may reproduce sexually or asexually. Growth of colonial forms takes place by a form of asexual reproduction through budding to form new polyps. Budding may occur by the division of an existing polyp (intratentacular budding) or by the formation of a polyp in the space between two existing polyps (extratentacular budding) (Richmond, 1996). *L. pertusa* and *Solenosmilia variabilis* grow by intratentacular budding, whilst other deep-sea species (e.g., *Enallopsammia* spp.) grow by extratentacular budding (Cairns, 1995). Corals may also reproduce by fragmentation, whereby pieces of a parent colony break off and continue to grow, forming new coral colonies. This process is important in the development of cold-water *L. pertusa* reefs by Wilson (1979b) and reviewed by Rogers (1999). In some corals, pieces of living tissue may regenerate from an otherwise dead coral skeleton, or may leave the coral skeleton, and swim, using cilia covering the epidermis, and settle to form a new colony in a process known as 'polyp bale out' (Sammarco, 1982; Krupp, 1983).

Sexually reproducing corals may have separate sexes (gonochoric) or may be hermaphroditic or may even display both life-history strategies where some individuals are single sex and some have both male and female gonads (Richmond, 1996). About 25% of shallow-water corals are gonochoristic, while the majority are hermaphroditic where reproductive biology is known (Fadlallah, 1983; Richmond and Hunter, 1990). Eight species, e.g., *L. pertusa*, have all been found to be gonochoric (Waller *et al*., 2002; Burgess and Babcock, 2005; Waller and Tyler, 2005), whilst three, e.g., *Caryophyllia ambrosia*, are all hermaphrodites (Waller *et al*., 2005). The octocorals *Corallium secundum*, *C. laauense* and the zoanthidean *Gerardia* spp. from deep-water habitats in Hawaii have also been found to be gonochoric (Waller and Baco-Taylor, 2005). Based on the limited knowledge to date, it appears that deep-sea corals show differences in sexuality to shallow-water hermatypic corals (Roberts *et al*., 2006). That only one genus displays hermaphroditism

probably reflects systematic constraints on life history, although it should be noted that the shallow-water *C. smithii* is gonochoric (Tranter *et al*., 1982).

Sexually reproducing corals show two modes of larval development, brooding or broadcast spawning. In brooding species, the eggs are fertilised internally and develop into planula larvae prior to being released. The larvae are able to settle and metamorphose immediately after being released (Richmond, 1996). In broadcast spawners, eggs and sperms are released into the water column where fertilisation and subsequent development take place. The eggs have to develop into larvae that must grow for a period of several weeks before being competent to settle. Counter intuitively, the larvae of many brooding, shallow-water tropical corals may have higher dispersal potential than those of broadcast-spawning species. This is because the larvae of brooding species often have zooxanthellae that supplement the energy reserves of the larvae and enable them to survive without settlement and metamorphosis for long periods of time (Richmond, 1996). Only about 15% of the shallow-water coral species studied are brooders, with the majority being broadcast spawners (Richmond, 1996). Timing of reproduction in shallow-water corals is often highly seasonal, taking place over a few months of the year or even just over a few days. In warm-water hermatypic corals where the spawning period is very short, it is often coupled to the lunar cycle (Richmond, 1996).

Twelve species of deep-sea coral, including *L. Pertusa,*, show broadcast spawning (Waller *et al*., 2002; Waller, 2005; Waller and Baco-Taylor, 2005; Waller and Tyler, 2005). Most of these species produce large-sized oocytes varying between 400 µm maximum diameter in *E. rostrata* and 750 µm in *F. marenzelleri*, suggesting leicithotrophic development. A range of species have smaller-sized eggs but some possess leicithotrophic larvae (Burgess and Babcock, 2005; Waller, 2005; Waller and Baco-Taylor, 2005). It is notable that all the species with smaller eggs are primary reef constructors. The production of leicithotrophic larvae is more common than planktotrophic larvae in deep-sea species (Gage and Tyler, 1991; Young, 1994). Both *Flabellum curvatum* and *F. impensum* off the Antarctic Peninsula are brooding species with very late stage larvae, that are probably competent to settle immediately or shortly after release (Waller *et al*., in press). Previously, it was thought that harsh ecological conditions at high latitudes favoured brooding of larvae (reviewed by Pearse, 1994). However, many Antarctic species have planktotrophic larvae and only some groups of organisms show a prevalence of brooding in their life histories (Pearse and Lockhart, 2004). The reasons for the prevalence of brooding in some groups are not fully understood, although to some degree it is a result of phylogenetic constraint. It may also be related to the geographic and the oceanographic history of the Antarctic and Sub-Antarctic (Pearse and Lockhart, 2004). *F. impensum* and *F. curvatum* also occur outside of the Southern Ocean in the SW Pacific and SW Atlantic, and *S. variabilis*, a non-brooding species, is found in the Southern Ocean.

The mean fecundity of the deep-sea corals that inhabit seamounts varies from a high of 3146 oocytes per polyp in *L. pertusa* to a low of 10 in *Madrepora oculata* (Waller and Tyler, 2005). The remaining species lie between these two extremes (Waller, 2005). To some extent, this is related to the size of the oocytes and the size of the coral polyps. Solitary corals have large polyps and can develop large number of large eggs, whereas colonial forms can produce large number of small eggs or low number of large eggs (Waller, 2005). The overall fecundity of colonial corals is potentially large.

The timing of reproduction in deep-sea corals that live on seamounts and banks also varies markedly. Some species show seasonal reproduction, such as *L. pertusa* in the NE Atlantic, which probably spawns in winter (January/February; Waller and Tyler, 2005) and *Gerardia* spp. in the North Pacific (Waller and Baco-Taylor, 2005). Others such as *M. oculata* in the NE Atlantic show periodic reproduction that is not seasonal (Waller and Tyler, 2005). Still others such as *F. marenzelleri* from the NE Atlantic, *C. lauuense* and *C. secundum* from the North Pacific, are quasi-continuous spawners, where reproduction is continuous but possibly with some variation in spawning intensity through the year (Waller *et al*., 2002; Waller and Baco-Taylor, 2005). The hermaphroditic *Caryophyllia* spp. that have been studied show a cyclicity of development of male and female gametes within individuals so that self-fertilisation is not possible (Waller *et al*., 2002). The timing of spawning in species of corals recorded as living on seamounts therefore varies markedly and is likely to be controlled by a range of environmental and genetic (phylogenetic) factors.

Age and growth of deep-sea corals on seamounts

Deep-water scleractinians can form ancient reefs through accumulation and repeated settlement on older coral skeletons over time. Schröder-Ritzrau *et al*. (2005) used U/Th dating to determine the ages of Atlantic deep-water corals exposed at the seabed. They found that seamounts off NW Africa, the low latitude Mid-Atlantic Ridge and the Azores had conditions suitable for coral growth during glacial times, as well as the interglacial periods, with coral samples spanning the past 50 000 years. In contrast, deep-water reefs from northern parts of the Atlantic were merely thousands of years old. All were of Holocene age, indicating that glacial periods were unfavourable for coral growth at high latitudes. Few geological cores have yet been analysed from deep-water reefs, but the current record for the oldest living reef comes from giant coral-topped mounds off Ireland that have been building up intermittently since the Pleistocene (De Mol *et al*., 2005).

Deep-water reefs are generating strong interest in climate change research because zooxanthellate scleractinians have been shown to provide important archives of seasonal variations in temperature, salinity, and productivity in shallow waters of the tropics (Tudhope *et al*., 2001; Cohen *et al*., 2004; Roberts *et al*., 2006). It is hoped that analyses of deep-water corals and the remains of their associated biota will provide a detailed understanding of subsurface oceanic circulation patterns as this is key to accurate predictions of future climate variability (Smith *et al*., 1997; Adkins *et al*., 1998; Thresher *et al*., 2004 López-Correa, 2005; Risk *et al*., 2005). The deep-water scleractinians examined for paleoclimate signals to date have complex internal banding patterns that makes extracting time series of environmental change difficult (Sinclair *et al*., 2005). However, the skeletons of deep-water gorgonians, antipatharians, and zoanthids can show a much clearer banding similar to tree-rings and this can be used to estimate age (Sherwood *et al*., 2005). Growth band studies (sclerochronology) of this sort require validation using radiometric analyses whereby naturally occurring radioisotopes are used to determine an independent estimate of age or growth rate. Such studies have revealed that the oldest known deep-water coral to date is Gerardia spp., a zoanthid from 620 m off Florida, carbon dated to 1800 years old (Druffel *et al*., 1995). Gorgonians can also be slow growing and long lived, the oldest known being fossil specimens of *Primnoa resedaeformis* from Georges

Bank dated as 320 years (Risk *et al*., 2002) and 700 ± 100 years (Sherwood *et al*., 2006). Andrews *et al*. (2002) dated a 112 years old *P. resedaeformis* colony in the Gulf of Alaska and noted that larger colonies in the vicinity were probably older.

Evidence shows that deep-sea corals have the potential to live for thousands of years and are typically slow growing (Andrews *et al*., 2005a), yet where food supply and water conditions are optimal some can grow quickly. For example, the scleractinian *L. pertusa* has rapidly colonised oil rigs and exhibited growth rates of up to 33 mm/year (Gass and Roberts, 2006). Recent carbon dating work on isidid corals by Roark *et al*. (2005) revealed ages of 75–126 years confirming the longevity of certain deep-water corals, although lead-210 dating of an isidid (*Lepidisis* spp.) from 690 to 800 m off New Zealand by Tracy *et al*. (2005) showed that it was 38–48 years old, indicating a linear growth rate of *ca.* 30 mm/year. Andrews *et al*. (2005b) used the same methods on another isidid (*Keratoisis* sp.), collected at 1425 m on Davidson Seamount off California. This colony was 97–197 years old and had grown about three times more slowly than the shallower New Zealand isidid, suggesting that food supply may limit growth at depth.

Role of corals in structuring seamount communities

Some of the corals that occur on seamounts and banks are capable of forming reefs. However, most of our knowledge on the ecology of deep-sea or cold-water coral reefs relates to frameworks constructed by *L. pertusa*. This species has a wide distribution, but to date, large complex reefs formed by *L. pertusa* have only been found in fjords, on the contin-ental slope and on slope or near-slope banks rather than oceanic seamounts[*]. *S. variabilis*, one of the main reef-forming corals, builds extensive frameworks on seamounts, along with several secondary reef-constructing species such as *M. oculata* and *Desmophyllum dianthus* (e.g., Koslow *et al*., 2001; Clark and O'Driscoll, 2003). Reefs formed by this species have been observed off New Zealand and Australia. There is also evidence of reefs on the Pacific–Antarctic Ridge and on a small seamount in Drake Passage in the Southern Ocean. Most corals occur on seamounts as thickets or isolated colonies. Although these may influence the diversity of the seamount habitat by structuring the environment, they are not reefs.

Cold-water coral reefs, like shallow-water tropical corals reefs, host a distinct community of associated species that contrast with the surrounding deep seabed in terms of taxonomic composition and biomass (Rogers, 1999; Freiwald *et al*., 2002). This is because the corals secrete calcium carbonate to form a complex three-dimensional skeleton that alters the local hydrodynamic and sedimentary regime (Freiwald *et al*., 2002). Such coral species are defined as being hermatypic and may be classed as 'ecosystem engineers' defined by Jones *et al*. (1994) as a species that alters the environment by its physical presence. The coral frameworks present a variety of sub-habitats, including coral rubble, sediment clogged coral framework, exposed dead coral framework and the living coral (Jensen and Frederiksen, 1992; Mortensen *et al*., 1995; Rogers, 1999; Freiwald *et al*., 2002).

The presence of a variety of substrata and habitats that are not present on surrounding deep-sea sediments explains the high diversity and contrasting faunal composition of

[*]See Supplementary Material for map

deep-sea coral reefs compared with the background communities (Rogers, 1999; Freiwald *et al*., 2002). The number of macrofaunal and megafaunal species and the density of organisms tend to be high on cold-water coral reefs compared to the surrounding habitats (Jensen and Frederiksen, 1992; Koslow *et al*., 2001; Jonsson *et al*., 2004; Thiem *et al*., 2006). For many groups of organisms, the diversity found in the few studies of deep-water coral reefs is comparable to those on shallow-water reefs, although data are very limited for both (Rogers, 1999). There are notable exceptions to this, and the diversity of reef-forming corals, fish and molluscs tends to be much lower on cold water than tropical coral reefs (Rogers, 1999). Many biophysical processes on deep-water and shallow-water, tropical coral reefs are similar, including processes of reef accretion and destruction (Rogers, 1999; Freiwald *et al*., 2002).

One of the main questions is how many species are endemic, or obligate associates of living or dead deep-sea coral communities. More than 1300 species have been described as associated with *L. pertusa* reefs in the NE Atlantic, although the vast majority of these occur in other habitats (Rogers, 1999; Roberts and Gage, 2003; Roberts *et al*., 2006). For example, in the NE Atlantic, fish species such as redfish (*Sebastes marinus*), tusk (*Brosme brosme*) and ling (*Molva molva*) occur both on and off *L. pertusa* reefs, although they may be more numerous and larger in reef habitats (Husebø *et al*., 2002). Between 24% and 43% of the 262 invertebrate species collected from *S. variabilis* reefs on the seamounts south of Tasmania were undescribed and about 16–43% thought to be endemic (Richer de Forges *et al*., 2000; Koslow *et al*., 2001). If seamounts conform to expectations of island biogeography, it is likely that they will recruit species from the regional species pool, which in the SW Pacific may be huge (see later and Chapter 13). In general, islands have a lower species diversity than the nearest mainland fauna (Vermeij, 2004), although the ratio of endemic to surrounding species varies and may be as high as 42%.

It is now recognised that other types of coral can form distinct habitats with associated communities of animals. In particular, large colonies of gorgonians can form dense stands (Auster *et al*., 2005). These have been located in the North Pacific, throughout Hawaii, along the Aleutian Island chain, and also in the Bering Sea and Gulf of Alaska (e.g. Stone, 2006). These habitats have been found to be rich in redfish (*Sebastes* spp.), shrimp, galatheid lobsters and other crustaceans (e.g. Stone 2006). They also host other attached suspension feeders such as crinoids, basket stars, sponges and other corals (e.g., Parrish and Baco, in press). NE Atlantic gorgonians *Acanthogorgia* spp. have been found to host the amphipod *Pleusymtes comitari*, thought to be an obligate commensal species (Myers and Hall-Spencer, 2004). The legs of the amphipod have special hooks to grip on to the coral. Predators that specialise on feeding on the polyps of the octocorals have also been identified, including starfish (*Hippasteria heathii*) and a nudibranch (*Tritonia exulsans*) (Krieger and Wing, 2002). Gorgonians and other corals also form dense populations in areas such as canyons and may also have a highly diverse associated fauna. *Paragorgia arborea* has been found to host up to 16 species of crustaceans and *Primnoa resedaeformis* 7 (Buhl-Mortensen and Mortensen, 2004).

Predatory fish may take advantage of the energetic environment of seamounts and other deep-sea habitats by feeding at certain times of day in the current and then resting in cryptic habitat, such as behind rocks, or amongst corals. Hundreds of the rockfish, *S. alutus*, have been observed resting amongst forests of sea whip corals (*Halipteris*

willemoesi) at night and then swimming above the corals during the day to prey on passing food items (Brodeur, 2001). Such behaviour may explain the association of many species of seamount fish with biogenic habitats, although there is evidence that any physical structure creating shelter from current may serve this function (Auster *et al.*, 2005; ICES, 2005).

Studies in the Hawaiian Archipelago on associations between black corals (*Antipathes* spp.) in shallow water and fish have indicated that many fish may routinely pass through the branches of coral colonies treating them as general habitat. A few species regularly used the coral for protection from perceived threats and only one species of fish was restricted to the branches of coral trees (Boland and Parrish, 2005). The fish communities of deeper slopes in Hawaii also use corals (*Gerardia* and *Corallium* spp.) as shelter interchangeably with non-biotic habitat (Parrish and Baco, in press). Taller coral colonies (*Gerardia* spp.) are more attractive to fish than other corals. In some cases, observations suggest that fish and corals may have similar habitat requirements on seamounts and banks (e.g., exposure to currents or areas with a high supply of planktonic food; Mundy and Parrish, 2004; Parrish and Baco, in press). Resolution of the question of importance of stands of gorgonians to fish species will require further detailed *in situ* observational studies and habitat classification (Auster *et al.*, 2005). The rich communities of animals associated with coral reefs, or forests of gorgonians or sponges may in themselves provide food for predators. Evidence from electronic tagging and submersible observations on banks off Hawaii indicate that Hawaiian monk seals (*Monachus schauinslandi*) may preferentially forage for fish amongst beds of deep-sea octocorals and antipatharians (Parrish *et al.*, 2002). Observations from submersibles have also suggested that some fish that occur on seamounts may feed on invertebrates associated with coral colonies or on the coral polyps themselves (Auster *et al.*, 2005). There may be a direct link between commercial fish species and benthic habitat-forming organisms (see also the 'feed-rest' hypothesis in Chapter 6). This means that fishing activities on seamounts may not only have the potential to directly remove target fish species but may destroy or severely reduce habitat essential for the existence of fish populations in these areas and negatively impact on the predators that feed on them.

Biogeography

Geographic and taxonomic coverage of sampling for corals

A total of 3215 species of corals have been recorded on seamounts, making them one of the best studied groups of animals in these habitats. The question arises as to whether such a dataset is informative in terms of patterns of biodiversity on seamounts. Previous studies have recorded species from only about 200 seamounts (Stocks, 2004). Estimates from satellite gravity maps indicate that there are probably 100 000 or more large seamounts (1000 m + elevation; Wessel, 2001; see Chapters 1 and 2), i.e., the number sampled is a small proportion of the total. In the present study, records of corals and stylasterids were obtained for 271 seamounts, banks and ridges, reducing to a total of 184 if shelf or continental slope-associated banks are removed from the dataset. This number of seamounts and banks is larger than the number from which cnidarians have previously been recorded

(84 in Stocks, 2004), but is still tiny compared to the overall number of seamounts in the world's oceans. The geographic distribution of records of corals from seamounts, banks and ridges makes it apparent that whilst some areas have been well sampled, such as around New Zealand, Hawaii, off western N America and in the NE and NW Atlantic, vast areas of the ocean remain unsampled (see Fig. 8.1). The present dataset contains only five records of corals from the entire Indian Ocean and all these are associated with
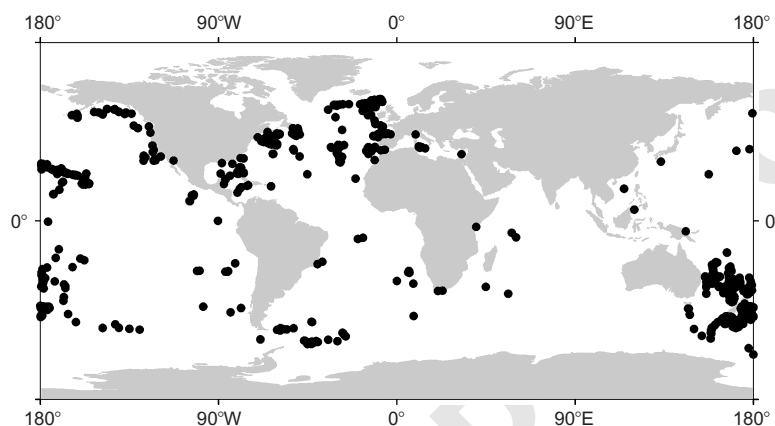

Fig. 8.1 Octocorallia global map of the distribution of the samples of corals on seamounts (dark circles) included in analyses of distribution and biogeography.

shallow banks. Large areas of the NE, W, equatorial and S central Pacific and S Atlantic Oceans have not been sampled. Some of these areas, especially the Pacific Ocean, contain the largest concentrations of seamounts in the world (Wessel, 2001; Stone *et al*., 2004).

The global deficiency of scientific expertise in coral taxonomy is another significant barrier to understanding the diversity of corals and many other organisms on seamounts. De Vogelaere *et al*. (2005) report that Davidson Seamount, off California, hosts at least 20 coral species, with *Paragorgia* spp. being abundant and forming large and dense patches. However, they only able to identify three other coral species to genus level and none to species. Many records obtained in the present study only identified corals to genus or family level, greatly decreasing the usefulness of the data in a global analysis of coral distribution and in the establishment of programmes to manage and minimise human impacts.

Global distribution

One of the most striking features of the occurrence of corals on seamounts and banks is that the majority of species have been observed only within one region of one ocean (Table 8.2). This is even considering land-locked seas, such as the Mediterranean and Caribbean as separate regions from the major oceans to which they are connected. This regionalisation partially reflects the poor sampling of seamounts in many parts of the world. Difficulties in identification of corals also mean that the true geographic distribution of many species remains unresolved. Recent analyses of mitochondrial DNA sequences from corals in the New Zealand region, for example, have identified haplotypes identical to

Table 8.2 Distribution patterns of corals (Scleractinia, Octocorallia, Antipatharia, Zoanthidea, Stylasterida) across oceans and regions within oceans.

Taxon/geographic scale	Scleractinia	Octocorallia	Antipatharia	Stylasterida	Zoanthidea	Total
Species occurring in one ocean or inland sea	218	156	27	64	14	479
Species occurring in two oceans or inland seas	30	5	7	4	0	46
Species occurring in three oceans or inland seas	4	0	0	0	0	4
Species occurring in one region in one ocean	204	134	26	63	13	440
Species occurring in two regions in one ocean	22	22	2	1	1	48
Species occurring in three regions in one ocean	5	0	0	0	0	5

Acanella arbuscula from the Atlantic (Smith *et al*., 2004), the only area in which this species is recorded as occurring on seamounts. Studies on seamount coral taxonomy show that many species occur in other habitats elsewhere in the world. For example, *F. lowekeyesi* is recorded from SW Pacific seamounts but is also known from the SW Indian Ocean. Despite the lack of coral records from seamounts for many parts of the globe, several regions have been sampled relatively well, especially the SW Pacific, the NE Pacific and the N Atlantic. If the distribution of corals on seamounts were widespread then this should be obvious, even within the limitations of the present dataset. Some coral species are endemic to specific regions and are commonly recorded on seamounts and banks.

The limitations of the dataset make it difficult and complex to explain the apparent regionalisation of the seamount coral fauna. A great variety of methods of sampling corals from seamounts and banks have been used from dredging to point sampling with submersibles. Sampling methodology is known to affect estimates of community diversity. The depth to the seamount or bank summit and the physical environment provided by different seamounts must influence coral distribution. The most obvious examples of this are zooxanthellate species, such as those belonging to the genus *Acropora*, which require sunlight and warm waters and will therefore only occur in regions where seamounts and banks with shallow summits occur in the tropics or sub-tropics such as the Caribbean and around Hawaii. Seamounts and banks also represent island-like patches of habitat that contrast strongly in their physical characteristics with the surrounding seabed that is at greater depth, may lie in a different oceanographic regime and is often composed of sediment. As such, seamounts may be expected to conform to the predictions of island biogeographic theory in terms of community assembly (MacArthur and Wilson, 1967) where distance to source populations, which are usually on the continental shelf or slope, the age of the seamount, the proximity to other seamounts and the size of the seamount play a critical role in determination of rates of species immigration, colonisation and extinction (see also Chapter 13).

Specific habitat availability on seamounts and island biogeography community dynamics may be sufficient to explain why the distribution of corals on seamounts does not reflect global occurrence of many species even within the sampling limitations of this study. It may also explain why the few detailed investigations of seamount biology have revealed relatively little similarity in the species composition of communities, even in

adjacent seamounts within chains or between seamounts located on different chains (e.g., Richer de Forges *et al*., 2000). Island biogeography predicts that the fauna of 'islands' will be a subset of that of the nearest source regions and this is consistent with at least some studies of seamount faunas. An example would be the megafauna of the Great Meteor Seamount (Piepenberg and Müller, 2004; reviewed by Wilson and Kaufmann, 1987). This contrasts with the high levels of diversity described for seamount communities in the SW Pacific, which include the South Australian Seamounts, those near New Caledonia and on Lord Howe Rise (Richer de Forges *et al*., 2000). However, it must be considered that the SW Pacific studies have taken place on the periphery of the most biologically diverse marine region in the world, the tropical Indo-West Pacific (e.g., Briggs, 2003). The fauna of the deep shelf, continental slopes and abyssal plains of this region are largely unexplored. Seamounts probably recruit species from the regional species pool and diversity is likely to reflect regional species diversity (Cornell and Lawton, 1992; Karlson *et al*., 2004; Witman *et al*., 2004; Chapter 13) that in this region are likely to be very high. This also may mean that point comparisons with small areas of seabed on the immediately adjacent continental slope may not be meaningful.

Another obvious aspect of the coral dataset is that very few species of corals occur across a very wide geographic area (Table 8.2). Only four species, *D. dianthus*, *S. variabilis*, *Stenocyathus vermiformis* and *M. oculata*, occur on seamounts in three oceans (see Supplementary Material for maps[*]). All the widespread corals are scleractinians, probably because these corals have a good ability to disperse by planktonic larvae, although this is unproven (see earlier). Three out of four of these species are also primary or secondary framework constructors in cold-water coral reefs. Other widespread species of scleractinians are also reef-building species and at least one of these, *L. pertusa*, has been observed to colonise remote oil platforms presumably by dispersal of pelagic planula larvae (Gass and Roberts, 2006). Why reef-building species should have such wide geographic distributions is unknown. Distributions may result from vicariance, which has left fragmented populations from a previously wider distribution. There is evidence that cold-water coral reefs have been eliminated from many areas as a result of climate change (e.g., Rogers, 1999; Remia and Taviani, 2005). It is also possible that the population dynamics of reef-forming species, or the environment in which they occur, selects for planktotrophic larval development that confers high dispersal ability for these species. The detailed systematics of such widely distributed species of coral also remains uninvestigated using molecular techniques and they may represent geographically separated sibling species.

Analysis of the species richness of corals on seamounts on a 10° latitude and 10° longitude grid shows that the SW Pacific has the highest species diversity irrespective of whether seamounts and banks are considered or just seamounts alone (Figs. 8.2 and 8.3). Other areas of high diversity include the NE Pacific and the NE Atlantic. However, plotting the number of species for each 10° × 10° box against the number of samples (Fig. 8.4) shows a strong relationship between sampling intensity and species richness. To try and correct for sampling intensity, the number of species for each 10° × 10° box was divided by the number of samples and re-plotted on the world map (Fig. 8.5). The results are in many ways the reciprocal of the plot of species richness, as for many areas

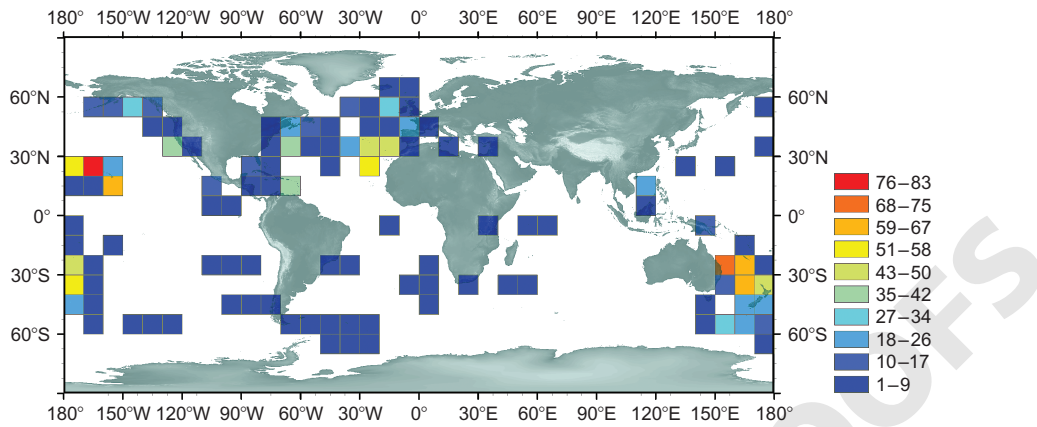*See Supplementary material on-line at ww.seamounts book.info

Fig. 8.2 Global species richness of corals on seamounts, banks, ridges and plateaus analysed on 10° × 10° grid of latitude and longitude. *Key*: Number of species; red: high diversity; blue: low diversity.
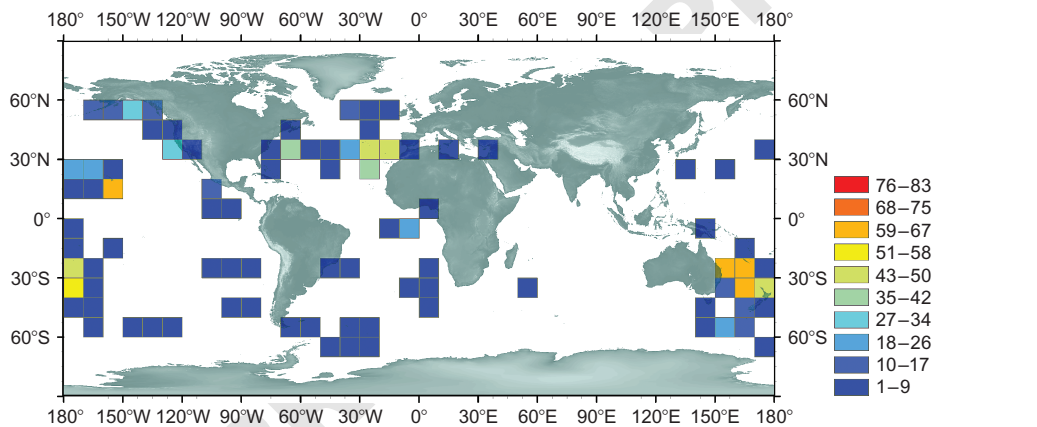

Fig. 8.3 Global species richness of corals on seamounts only, analysed on 10 °× 10° grid of latitude and longitude. *Key*: Number of species; red: high diversity; blue: low diversity.

of low sampling effort, a relatively high number of species per sample are identified. This is expected from species-accumulation curves, as the number of species detected in a few consecutive samples rises very steeply and only levels off when the regional fauna has been well sampled. It is notable that the SW and NE Pacific areas still have quite a high species richness to sampling ratio. The species-rich boxes in the NE Atlantic (Figs. 8.2 and 8.3), however, have a low species richness to sampling ratio in Fig. 8.5. This indicates that high sampling effort has probably over-represented the importance of parts of this area in terms of species richness. This is confirmed by detailed examination of the values that fall well above and well below the trend line in Fig. 8.4. Grid boxes from the NE and SW Pacific show a high number of species per sample. Those from the N Atlantic show low number of species per sample, except one off SE New Zealand that probably represents a well-sampled area or an area where samples are dominated by a few abundant species. The northern N Atlantic region not only shows low species richness, but also a
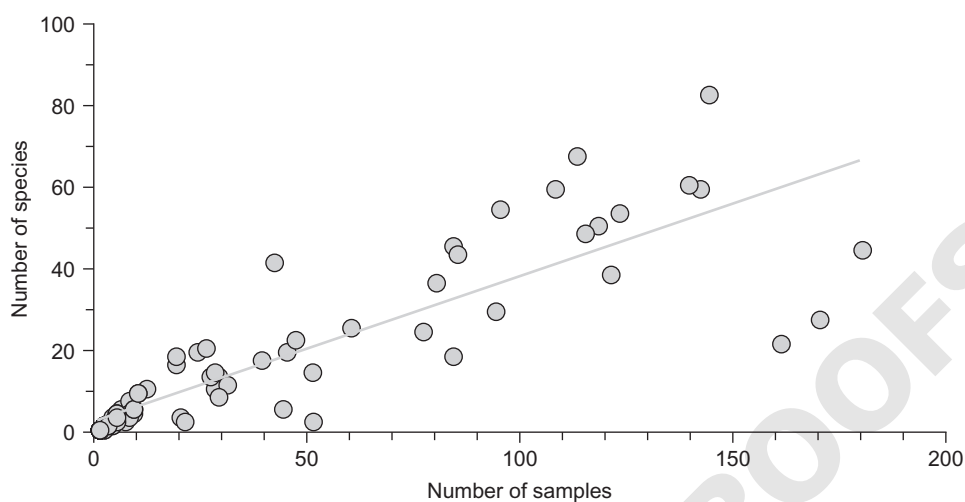
Fig. 8.4 Graph of number of samples vs number of species found on seamounts and banks in each $10° \times 10°$ box of a global grid. Line of best fit shown.

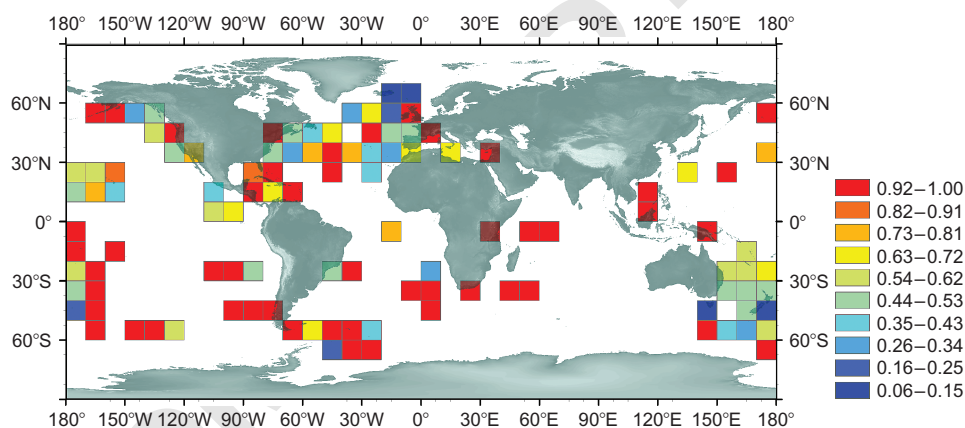**Fig. 8.5** Ratio of number of samples over number of species of corals observed on seamounts and banks in each $10° \times 10°$ latitudinal and longitudinal box of a global grid. Key at lower right: Red: high number of species per sample; blue: low number of species per sample.

low species richness to sample ratio, possibly indicating that this region has a genuinely low diversity. The Arctic is known to have an impoverished fauna as a result of cycles of glaciation (Gage and Tyler, 1991).

The SW Pacific region is on the periphery of the Indo-West Pacific biodiversity hotspot, the most species-rich area of the world's oceans, including the 'coral triangle', the greatest concentration of shallow coral reef biodiversity (e.g., Bechtel *et al.*, 2004; Wilkinson, 2004; Briggs, 2005; Heads, 2005). This region, which had its origins in the Tethys Sea and was established by the early Miocene, has acted as a centre for speciation in shallow water and subsequent species dispersal across the SW Pacific (Briggs, 2000, 2003, 2005). Onshore–offshore patterns of speciation likely had a positive influence on the diversity of the deep seas in this region including the SW Pacific (Zezina, 1997; Briggs, 2003;

Chapter 13). The W Pacific is also the location of the greatest number and concentration of seamounts anywhere in the world (Wessel, 2001; Chapters 1 and 2). It has been suggested that habitat size in islands is proportional to the number of island 'units' in an area if within-island dispersal takes place (Holt, 1992; Cook *et al*., 2002). Therefore, habitat availability may also partially explain the high diversity of corals in the SW Pacific.

The high species richness of the NE Pacific is more difficult to explain. This may be a sampling artefact as the region includes many recent records from banks and seamounts in the vicinity of the Hawaiian Islands. However, this region is likely to be influenced by species dispersing from the Indo-West Pacific, as with the SW Pacific. Observations on species from other marine habitats indicate that the Hawaiian Islands receive species from several other regions, including the Ryuku Islands, Japan, in the NW Pacific and from Polynesia to the south and east (Vermeij, 2004). Analysis of mitochondrial DNA sequence variation amongst species of bamboo corals of the sub-family Keratoisidinae from an area off New Zealand in the SW Pacific and the Hawaiian Islands showed identical haplotypes occurring in both regions (Smith *et al*., 2004). This suggests that at least some species have the capacity to disperse even to the distant seamount chains in the Pacific Ocean. It is possible, therefore, that corals have colonised the seamounts and banks around the Hawaiian Islands from a number of other regions over a wide area of the Pacific, possibly using seamount chains as stepping stones (Hubbs, 1959; Rogers, 1994).

A peculiarity of the NE Pacific data compared with that of the SW Pacific is the prevalence of species of octocorals compared to scleractinians (Table 8.3). There is a notable lack of species records of scleractinians from the NE Pacific and those that have been recorded are mainly from 'banks', shallower features mainly in the Hawaiian Islands. Octocorals are

Table 8.3 Number of species of the different coral groups that occur on (a) seamounts and (b) banks in different geographic regions.

Group/region	Scleractinia		Octocorallia		Antipatharia		Zoanthidea		Stylasterida	
	a	b	a	b	a	b	a	b	a	b
NEA	48	24	27	3	8	1	–	1	7	4
NWA	9	9	7	17	2	–	1	2	–	–
SEA	10	–	1	–	–	–	–	4	–	–
SWA	5	5	1	–	–	–	–	–	–	–
Med	2	7	–	–	–	–	–	–	–	–
Car	–	31	–	21	–	8	–	3	–	3
NEP	15	29	54	25	13	9	1	1	1	–
NWP	3	5	3	19	3	–	–	1	–	2
SEP	3	–	–	–	–	–	–	–	–	–
SWP	108	17	20	1	–	–	–	–	46	19
SCS	–	18	–	–	–	–	–	1	–	–
Cel	–	–	–	1	–	–	–	–	–	–
WIO	–	3	–	–	–	–	–	1	–	–
EIO	–	1	–	–	–	–	–	–	–	–
SO	8	–	4	–	1	–	–	–	4	–

NEA: North East Atlantic; NWA: North West Atlantic; SEA: South East Atlantic; SWA: South West Atlantic; Med: Mediterranean; Car: Caribbean; NEP: North East Pacific; NWP: North West Pacific; SEP: South East Pacific; SWP: South West Pacific; Cel: Celebes Sea; SCS: South China Sea; WIO: Western Indian Ocean; EIO: Eastern Indian Ocean; SO: Southern Ocean.

more diverse in the NE Pacific and occur mainly on seamounts, although in the SW Pacific there are relatively few species. It is tempting to ascribe these differences to bias in collecting and identifying animals, but submersible observations in the Hawaiian Islands confirm the relative abundance of octocorals compared to scleractinians (Baco, Personal observation). It is likely that the changes in relative species diversity of different coral groups between these regions reflect differences in the physical characteristics of the seamounts and the biological and the physical oceanographic settings in which they occur (e.g., see Rowden *et al.*, 2005). In particular, the depth of the aragonite saturation horizon (ASH) is shallow in the N Pacific compared to other ocean regions such as the N Atlantic. Higher dissolution rates of aragonite in the N Pacific are likely to make this region less favourable for scleractinian corals and for formation of cold-water coral reefs (Guinotte *et al.*, 2006; Roberts *et al.*, 2006). Octocorals are less affected by a shallow ASH as their skeletons are formed by calcite. The extreme geographic isolation of the Hawaiian Island chain may also select for colonisation by octocorals from distant sources of species because of the life-history characteristics of these species. The differences in the biology of these groups may also be related to the occurrence of octocorals in deeper water than scleractinians (see later).

Sampling intensity has probably led to an overestimate of relative species richness of the N Atlantic in this study. The coral fauna of seamounts, however, is well developed and the presence of many banks located on the continental slopes of this region, beneath bands of high productivity surface waters associated with the shelf break (e.g., Pingree and Mardell, 1981; Holligan and Groom, 1986), may have provided large areas of suitable habitat for many coral species. Tropical regions, such as the W Atlantic, may have acted as evolutionary centres of origin for the Atlantic deep sea (Briggs, 2003). This hypothesis cannot yet be tested as little is known about tropical and sub-tropical W Atlantic seamounts and other deep-sea habitats with the exception of hydrocarbon seeps. A further source of species may have been the Great Trans-Arctic exchange between the N Pacific and Atlantic Oceans (Briggs, 1995). Several cold-water scleractinians and octocorals found in the North Atlantic also occur in the North Pacific. Dispersal *via* this route may have occurred although this is unproven.

Latitudinal patterns of diversity

Examination of the latitudinal distribution of species of corals on seamounts suggests that species richness peaks at mid-latitudes (20–40° N/S), with low values at the poles and very low values at equatorial latitudes (Fig. 8.6). This is not consistent with reports of parabolic patterns of species richness with latitude in marine species, where peak biodiversity is recorded at low latitudes and decreases progressively towards the poles (e.g., Hillebrand, 2004; Witman *et al.*, 2004). Note that the latitudinal diversity in shallow benthic communities reported by Witman *et al.* (2004) shows high diversity values at mid-latitudes and moderate-to-low values at the equator despite reporting parabolic patterns of species richness with latitude (Fig. 3 of Witman *et al.*, 2004). Seamount coral diversity would appear to be congruent with latitudinal biodiversity patterns in large, oceanic predators (Worm *et al.*, 2003). However, examination of the latitudinal pattern of distribution of sampled seamounts shows the same broad pattern as species richness in corals. A hypothesis that
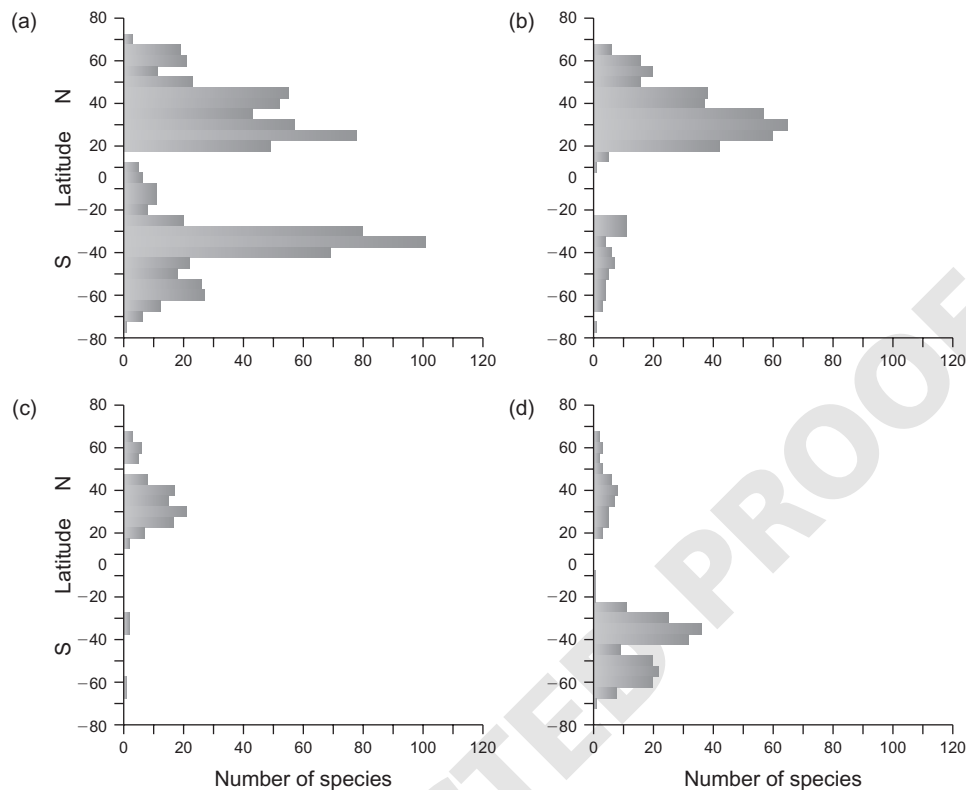
Fig. 8.6 Distribution of number of species at different latitudes: (a) Scleractinia, (b) Octocorallia, (c) Antipatharia and (d) Stylasterida.

the latitudinal pattern of species richness reflects sampling intensity of seamounts cannot be rejected. To some extent, this may reflect the actual distribution of seamounts (e.g., see maps in Stone *et al.*, 2004), although it is likely that it simply reflects lack of scientific sampling effort on equatorial seamounts.

Comparison of the latitudinal species richness of corals (Fig. 8.6) with the number of seamounts (Fig. 8.7) does reveal some differences. The species richness of corals at 20–30° N and 25–35° S does seem to be higher than would be expected simply from the number of seamounts and banks sampled. These latitudinal bands correspond to the SW Pacific and NE Pacific biodiversity hotspots; 45–55° N and 05–15° N appear to have low diversities given the number of seamounts and banks. However, the number of sites sampled in equatorial regions and high latitudes is so low that it is not possible to place any confidence in estimates of species richness.

Depth distribution

An analysis of variance using the general linear model (GLM) was used to compare the depth distribution of the different groups of corals. This was done by estimating the maximum and mean depths for all species and testing the hypothesis that the coral group (scleractinian, octocoral, antipatharian, stylasterid) was a predictor of the depth of distribution
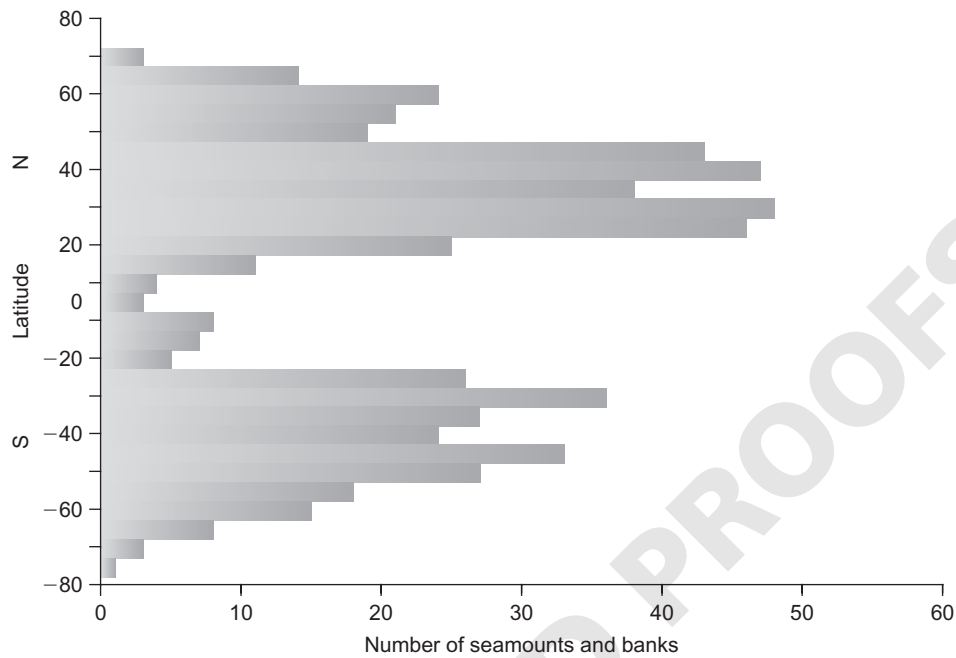
Fig. 8.7 Number of seamounts sampled at different latitudes.

of species. Data were root transformed to normalise the residuals. When this analysis was carried out on the entire dataset, it showed that the depth distributions were significantly different between the four coral groups ($p<0.001$; Table 8.4). Pairwise analyses showed that the depth distribution of scleractinian and stylasterid corals were not significantly different. Likewise, depth distributions of octocorals and antipatharians were not significantly different, although this analysis was weak given the poor sample size for antipatharians. The GLM analyses showed that depth distributions of scleractinians and

Table 8.4 Analysis of variance using GLM of the maximum and mean depths of distribution of species of Scleractinia, Octocorallia, Antipatharia and Stylasterida.

		F	p	R^2 (adj.) (%)
All data	Maximum	8.98	<0.001	5.67
	Mean	18.21	<0.001	11.48
Scleractinia vs Octocorallia	Maximum	18.44	<0.001	5.76
	Mean	46.78	<0.001	13.13
Scleractinia vs Antipatharia	Maximum	5.04	0.026	1.89
	Mean	6.52	0.011	2.56
Scleractinia vs Stylasterida	Maximum	0.24	0.624	0
	Mean	0.01	0.921	0
Octocorallia vs Antipatharia	Maximum	0.05	0.823	0
	Mean	1.51	0.220	0.35
Octocorallia vs Stylasterida	Maximum	16.25	<0.001	7.54
	Mean	25.35	<0.001	11.52
Stylasterida vs Antipatharia	Maximum	5.44	0.022	4.51
	Mean	5.05	0.027	4.14

stylasterids were significantly different from both octocorals and antipatharians (Table 8.4) (see Supplementary Material for more details).

These analyses demonstrate that the depth of a seamount will have a significant influence on the composition of the coral communities present. This may be the case for other groups of sessile organisms. However, it should be noted that even for mean depths, the R^2 values for the GLM indicate that taxonomic groups only explain 10–13% of the variation and that many other factors, such as the physical environment of a seamount and distance to the sources of colonisation, will also determine species composition (Rowden *et al.*, 2005). The reasons for significant differences in the depth distribution of species are complex but likely related to the ASH depth, the quantity and abundance of food at different depths and the nature of substrata available for attachment of species (see earlier comments).

Vulnerability and conservation

Harvesting of precious corals

Several octocorals, zoanthids and antipatharians are highly valued as a raw material for making jewellery and decorative objects. These species have been harvested from seamounts and islands in the vicinity of Hawaii since the 1950s and from the Emperor Seamount chain since the 1960s. These corals are all slow-growing, long-lived species that have low levels of natural mortality and recruitment (see above; Grigg, 1984). As a result, populations can only sustain a very low level of harvesting. The history of precious coral fisheries is one of frequent depletion (Grigg, 1984, 1986). Apart from the direct impacts of such fisheries on the target species, tangle-net dredges cause significant damage to other benthic sessile megafauna. The use of coral beds as foraging areas for the Hawaiian monk seals (see above) also means that such fisheries may impact on this extremely rare and endangered species.

Fishing

The South Australian Seamounts provide striking evidence for the impact of trawling on deep-water coral reefs. These seamounts have been subject to intensive trawling for orange roughy (*Hoplostethus atlanticus*) and oreo (*Pseudocyttus* spp., *Allocyttus* spp., *Neocyttus* spp.). On the most intensively trawled seamounts, the deep-water coral reefs, formed mainly by *S. variabilis*, have been totally removed or reduced to rubble (Koslow and Gowlett-Holmes, 1998; Koslow *et al.*, 2001). Deeper unfished seamounts hosted a rich deep-water coral reef community with a high proportion of undescribed and potentially endemic species. Photographic surveys on seamounts off New Zealand also identified a negative correlation between trawling intensity and the coverage of coral frameworks formed by *S. variabilis* (Clark and O'Driscoll, 2003). Trawling intensity, especially on small seamounts, has been found to be extremely intense with up to 17 400 km of tows per km2 of seamount summit, explaining the large-scale destruction of coral communities on some seamounts (O'Driscoll and Clark, 2005). In many other parts of the world where trawling has been observed to coincide with the occurrence of cold-water corals, large bycatches

of corals have been observed in the fisheries, and there has been photographic evidence of widespread destruction of benthic communities (reviewed by Freiwald *et al*., 2004).

As discussed, deep-sea corals take thousands of years to develop. Data on the recruitment of the larvae of deep-sea corals are very scarce, although at least one study on *Primnoa* spp. in the Gulf of Alaska has suggested that this may be sporadic (Krieger, 2001). Genetic and reproductive studies suggest that trawling can reduce deep-water coral colonies to a size where sexual reproduction is no longer viable (Le Goff *et al*., 2004). Given these factors, recovery of deep-water corals reefs from significant trawling impacts is likely to be extremely slow and where the habitat is altered may never happen (Hall-Spencer *et al*., 2002). The environmental impacts of trawling have a high risk of causing species extinction on seamounts and other deep-sea areas if they possess endemic species. In addition, whilst the links between the abundance of commercially valuable species of fish and the presence of coral communities are unproven the possibility still remains.

Climate change

The interaction between the background current field, the pelagic ecosystem and the communities living on or around seamounts is particularly strong (Rogers, 1994; Genin, 2004). In the past, natural climate change has dramatically affected the distribution of deep-sea corals (Rogers, 1999). It is likely that present climate change, driven by the burning of fossil fuels, will also impact the distribution of deep-sea corals through local and regional changes in primary productivity, organic carbon flux, the position and strength of major ocean currents and as a result of ocean acidification (Glover and Smith, 2003; Guinotte *et al*., 2006). Ocean acidification is of particular concern as over the next 100 years there may be marked changes in the depth of the ASH of the oceans, especially in the Southern Ocean, Sub-Arctic Pacific and northern N Atlantic (Orr *et al*., 2005). The effects of under-saturation of carbonates on corals are not well understood, but will at least decrease the rate of calcification of cold-water corals and will become corrosive to dead coral skeletons that are composed of aragonite, that form most of the habitat of deep-sea reefs. Overall, there may be large-scale changes in the faunal composition of seamount communities, especially where corals play a role in structuring the environment and providing habitats for other species.

Conclusions

Corals are important components of seamount ecosystems in terms of their diversity and their role in providing habitat for other species. It is likely that trophic focusing plays a significant role in maintenance of seamount coral communities. Other physical factors at scales from metres to thousands of kilometres also play significant roles in determining the distribution of coral on seamounts. The different coral groups respond to these factors in contrasting ways, leading to differences in regional and vertical distribution. Knowledge of the life history of corals on seamounts is limited, although patterns of sexuality, larval development and timing of reproduction vary amongst the species that have been studied. It is now understood that many species of deep-sea corals are slow growing

and long lived. The conservative life history of corals and their fragility means that they are vulnerable to impacts from deep-sea fishing, especially trawling. However, corals are also sensitive to changes in the physical environment and the effects of global climate change represent a significant threat to corals on seamounts and other habitats globally.

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Author queries

1. Please provide the "plane of sympasium" for the reference 'Andrews et al. (2005b).
2. Please update the reference 'Parrish and Baco' and 'Waller et al.'

UNCORRECTED PROOFS