

The Ecology of Seamounts: Structure, Function, and Human Impacts

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biodiversity, connectivity, trophic structure, recovery, conservation, deep sea

Abstract

In this review of seamount ecology, we address a number of key scientific issues concerning the structure and function of benthic communities, human impacts, and seamount management and conservation. We consider whether community composition and diversity differ between seamounts and continental slopes, how important dispersal capabilities are in seamount connectivity, what environmental factors drive species composition and diversity, whether seamounts are centers of enhanced biological productivity, and whether they have unique trophic architecture. We discuss how vulnerable seamount communities are to fishing and mining, and how we can balance exploitation of resources and conservation of habitat. Despite considerable advances in recent years, there remain many questions about seamount ecosystems that need closer integration of molecular, oceanographic, and ecological research.

INTRODUCTION

Seamounts are widespread and prominent features of the world's underwater topography, with estimates of as many as 200,000 depending on the definition used with respect to elevation (e.g., Wessel 2001, Kitchingman et al. 2007, Hillier & Watts 2007)—here we adopt an “ecological” definition that includes seamounts, knolls, and hills (Pitcher et al. 2007). An increasing amount of research has described their biological communities and assessed patterns of benthic biodiversity and marine biogeography. In parallel, concerns have developed about the vulnerability of seamount communities to human impacts, especially with the development of large-scale bottom trawl fisheries in the deep sea in recent decades and the prospect of future seabed mining.

A number of review papers have been published over the years that summarize an evolving understanding of seamount ecology. Major compilations and reviews include those of Keating et al. (1987), Rogers (1994), and Pitcher et al. (2007), with a recent paper by McClain (2007) addressing a number of seamount issues. Since 2005, many studies have been coordinated by the international Census of Marine Life program on seamounts, “CenSeam,” and in this review, we address some of the most fundamental questions about seamount processes. These include patterns of benthic biodiversity and connectivity, structural and functional aspects of seamount ecosystems, resource use, and aspects of how to reconcile seamount exploitation and conservation. The review focuses primarily on benthic communities and follows the framework of the eight principal scientific questions developed and addressed during the CenSeam program.

THE SCIENCE QUESTIONS

(1) Differences in Community Composition and Diversity between Seamounts, and Seamounts-Continental Slope

Seamounts are not all the same; they differ in form, size, depth, and location (Rowden et al. 2005), and thereby alter local environmental and biogeographical conditions and faunal composition in distinct ways. At macroecological scales, the benthic fauna broadly reflects the regional species pool present on neighboring seamounts and continental margins (e.g., Ávila & Malaquias 2003, Samadi et al. 2006, Hall-Spencer et al. 2007, McClain et al. 2009). Seamount faunas respond to many of the same large-scale oceanographic gradients and anomalies as slope or abyssal faunas. They exhibit, for example, the same latitudinal turnover in species composition from tropical to subantarctic environments (O'Hara 2007), reduced species richness in oxygen-minimum zones (Wishner et al. 1990), and reduced coral habitat suitability in areas with shallow aragonite saturation horizons or low primary production (Tittensor et al. 2009).

Benthic community composition on seamounts is depth stratified, reflecting environmental gradients that correlate with depth, such as temperature, oxygen concentration, food availability, and pressure (see section 3). Longhurst's (1998) observation that there is as much marine faunal change over 1000 m vertically as over 1000 km horizontally is likely to also apply to seamounts.

The restriction of most marine animals to a limited bathymetric range (e.g., Rex et al. 1999) implies that their available habitat will be fragmented over areas of undulating seafloor, including isolated seamounts. This has led to speculation that seamounts may act as biogeographical islands (Hubbs 1959), with their fauna assembled from the same processes and following the same assembly rules that are theorized to occur on terrestrial islands (MacArthur & Wilson 1967, Simberloff & Wilson 1969, Diamond 1975). Although many of these processes are difficult to test in the deep sea, there have been attempts to estimate levels of endemism on seamounts.

A few studies have asserted that high-levels of endemism may be a feature of seamounts (e.g., Richer de Forges et al. 2000, Koslow et al. 2001, Stocks & Hart 2007). However, it is difficult to distinguish between true local endemism and sampling biases, particularly those arising from the occasional collection of rare but widespread species (O'Hara 2007, McClain 2007). Other studies have reported relatively few endemic species (Samadi et al. 2006, Hall-Spencer et al. 2007), sometimes no more than expected from equivalent areas on the continental slope (O'Hara 2007), although this may be taxon specific (Xavier & van Soest 2007).

Many species found on seamounts are widely distributed within their preferred depth range (Smith et al. 2004a, Samadi et al. 2006, McClain et al. 2009), suggesting that these species are good dispersers. Some seamount species have global or near-global distributions, including reef-building scleractinian corals (*Lophelia pertusa*, *Solenosmilia variabilis*, and *Madrepora oculata*) (Roberts et al. 2006) and fish such as orange roughy (*Hoplostethus atlanticus*) (Francis & Clark 2005). Many deep-sea species are lecithotrophic, although the short larval phase (just a few days) that is common in shallow water is not necessarily the case for deep-sea species. For example, Antarctic lecithotrophic larvae have been maintained for over 100 days in cold water aquaria (Emlet et al. 1987). Nevertheless, species richness (e.g., Leal & Bouchet 1991) or the degree of similarity between seamount assemblages (e.g., Parin et al. 1997) has been found to decrease with distance from the continental margin for some seamount chains and taxonomic groups.

It has also been suggested that seamounts are diversity hotspots, possessing benthic assemblages with particularly high species richness (Samadi et al. 2006). Comparing species richness of seamounts and the continental slope is often complicated by sampling artifacts, and to overcome this O'Hara (2007) compared levels of ophiuroid species richness between seamount and nonseamount areas, randomly generating nonseamount populations from areas and depth ranges that reflected the typical sampling profile of seamounts. Seamounts did not show elevated levels of species richness, and there were few species restricted only to seamounts. However, although they share many species, assemblages differ between seamounts and slopes where equivalent samples have been taken (e.g., Hall-Spencer et al. 2007, O'Hara et al. 2008, McClain et al. 2009). On temperate NE Atlantic seamounts, many of the species are characteristic of oceanic islands in the region and make up a significantly different coral assemblage to that recorded on the continental slope (Hall-Spencer et al. 2007). Along the southern margins of Australia and New Zealand, the cold-water coral *Solenosmilia variabilis* can form large reeflike thickets on the seamounts that are largely absent from the continental slope (**Figure 1**). Coral thickets contain a distinctive ophiuroid fauna (O'Hara et al. 2008) that potentially benefits from the shelter or enhanced food supply provided by the coral matrix (Roberts et al. 2006). Although these ophiuroids do not appear to be obligate commensals of *Solenosmilia*, they are consistently associated with this coral over large distances (i.e., thousands of kilometers) (O'Hara et al. 2008). In contrast to the coral thicket communities, seamount samples dominated by octocorals, antipatharians, stylasterids, and/or sponges were more similar to those found on hard substrata on continental slopes (O'Hara et al. 2008). McClain et al. (2009) found Davidson seamount off the west coast of the United States had a similar faunal composition to the adjacent slope area, but that the relative abundance of taxa differed strongly between habitats.

Soft sediments dominate some seamounts, particularly flat-topped guyots and banks, and the fauna of these habitats can be similar to neighboring continental slopes (e.g., Gillet & Dauvin 2000, Ávila & Malaquias 2003). However, these seamounts can be important for many species, even though elements of the fauna may be shared with other habitats (Roberts et al. 2006, O'Hara et al. 2008) and potentially serve as source populations for neighboring environments (McClain et al. 2009).

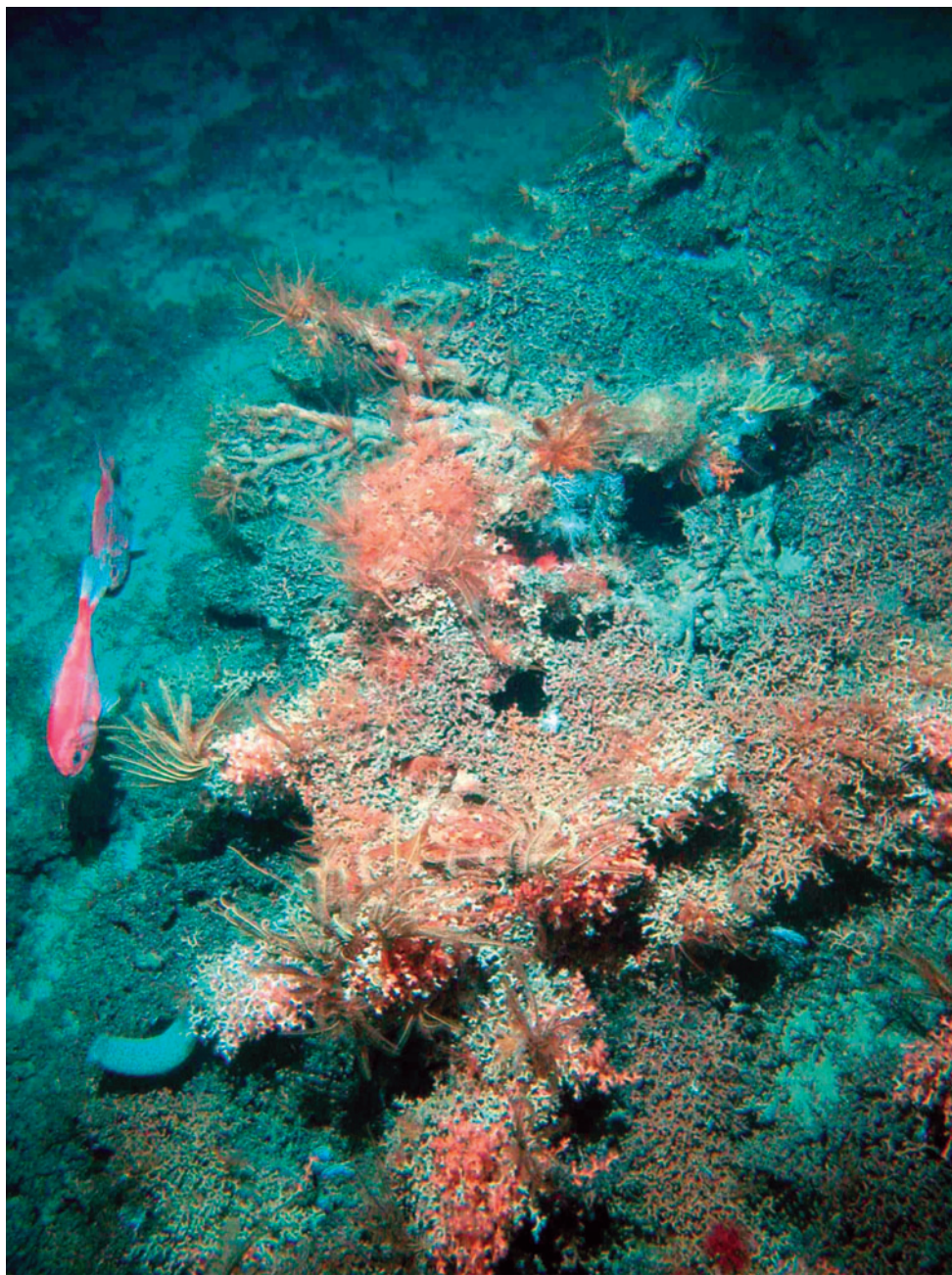


Figure 1

Stony coral faunal community at 950 m depth on a small seamount off New Zealand. Patches of *Solenosmilia variabilis* host featherstars and sponges, with orange roughy swimming close to the seafloor (Photo: NIWA).

(2) Connectivity of Fauna on Seamounts

Understanding patterns of evolution, species richness, and population dynamics of the biological communities of seamounts requires an understanding of connectivity between seamounts at a range of temporal and spatial scales. The factors that influence dispersal and connectivity between populations include a range of extrinsic factors, such as (a) the physical structure of the oceans (hydrographic retention mechanisms, currents, etc.), (b) environmental factors influencing development time and larval survival (e.g., temperature, availability of food, presence of predators), (c) the presence of suitable habitat when larvae become competent to settle, and (d) factors influencing postsettlement survivorship, which may be partially determined by larval condition (Cowan & Spangaugle 2009). Interactions of intrinsic biological features of taxa with the biophysical features of the environment are responsible for large variations in dispersal distances between species. Whether a species is sessile, whereby dispersal is through advection of eggs, larvae, and postlarvae, or is mobile, with dispersal also possible through juveniles or adults, is an important driver of dispersal distance (e.g., Bradbury et al. 2008) and subsequently seamount community composition.

The connectivity of seamount populations has been considered primarily in the context of seamounts resembling island systems with elevated levels of endemism per prevailing theory (see section 1). However, some precautions apply. First, present levels of connectivity, apparent from genetic studies of limited seamount fauna, may not represent the broader taxonomic composition of a given seamount. The presence of shared taxa among seamounts and other habitats does not automatically imply modern connectivity, which requires direct genetic testing to confirm (see Rogers et al. 2006, von der Heyden et al. 2007). Second, it is clear that despite a large number of studies, connectivity is poorly understood in nearshore or even littoral communities, let alone in offshore seamounts. Hence, making generalizations about connectivity and levels of endemism among seamounts is difficult and can be misleading. The discussion here of genetic connectivity studies on seamounts recognizes explicitly that additional research is needed.

The majority of studies on the genetic connectivity of seamount populations have been undertaken on commercially fished species. These studies have generally shown patterns of genetic homogeneity at oceanic or at regional geographic scales among populations sampled on seamounts, as well as the slopes of oceanic islands and continental margins (e.g., Martin et al. 1992, Sedberry et al. 1996, Hoarau & Borsa 2000). However, at the regional scale, genetic differentiation has been identified between populations of fish and cephalopod species located on the continental margin of Europe and the Azores Islands on the Mid-Atlantic Ridge (e.g., Logvinenko et al. 1983, Brierley et al. 1995, Shaw et al. 1999, Aboim et al. 2005, Stockley et al. 2005). It has also been shown for Patagonian toothfish, *Dissostichus eleginoides*, in the Southern Ocean, where genetic differentiation was detected between seamount and nonseamount populations (Rogers et al. 2006), and separation distance appeared useful in explaining some of the results from Ob, Speiss, and Meteor seamounts in the Indian Ocean. Distance was also a likely factor for significant genetic differentiation between populations of the lobster *Jasus tristani* on Vema Seamount compared to those on the Tristan da Cunha Archipelago and Gough Island (von der Heyden et al. 2007).

For noncommercial seamount invertebrates, there are also mixed patterns of genetic connectivity. Analyses of mitochondrial genes from corals of the family Keratoisidae from across the Pacific Ocean revealed widespread occurrence of haplotypes over large oceanic distances (Smith et al. 2004a). In contrast, the precious coral, *Corallium lauense*, on Hawaiian seamounts and islands showed low but significant genetic differentiation within continuous coral beds, between beds on the slopes of the same island or seamount, and between islands or islands and seamounts (Baco & Shank 2005). This suggests largely self-recruiting populations, with occasional long-distance

dispersal. Samadi et al. (2006) found genetic homogeneity in four species of squat lobster from nine seamounts and the slope of New Caledonia. Only one gastropod species, with a nonplanktotrophic developmental mode, showed significant genetic differentiation among the sampled seamounts, suggesting that early life history is important in determining the levels of connectivity among seamounts. Studies of populations of invertebrates inhabiting hydrothermal vents on ridges, seamounts, and knolls also demonstrate significant genetic differentiation at scales from thousands of kilometers (e.g., Wantanabe et al. 2005), to small distances (<100 km) when strong hydrographic barriers limit dispersal (e.g., Smith et al. 2004b).

Genetic studies on connectivity among seamount and other populations, while critical for the design and implementation of conservation and management efforts, must be interpreted with caution. Studies based on conserved genetic loci and/or on distant populations may reflect largely historical patterns of species dispersal and colonization, and may not resolve current levels of genetically effective migration. However, genetic studies do provide evidence that populations of organisms on seamounts demonstrate a large variation in distances over which dispersal may occur. Life history clearly influences connectivity, and complex hydrography around seamounts and/or larval behavior can lead to larval retention and less consistent patterns of connectivity compared to deeper waters, where currents are considered more uniform and predictable (Cowan & Sponaugle 2009).

(3) The Role of Environmental Factors in Diversity and Species Composition of Seamount Fauna

Benthic assemblages on seamounts differ across multiple spatial scales, ranging from compositional differences among habitat patches on a single seamount to totally different faunal assemblages between seamounts on different ridges and ocean basins. Some of the main factors that determine the overall environmental conditions for seamount biota (here considering principally mega- and macroinvertebrates) include light levels; the productivity of the overlying water; the hydrodynamic regime; the chemical nature of the water column; the geomorphology of the seamount; geological origin and age, which can dictate substratum type; and volcanic/hydrothermal activity. Some of these factors are related to water depth, making depth a frequently invoked proxy for describing differences in assemblage composition among seamounts (e.g., O'Hara 2007, Rogers et al. 2007) and elsewhere in the deep sea (Carney 2005). In fact, at the scale of the individual seamount, perhaps the most obvious changes in the composition of benthic assemblages are related to depth. Typically, light, temperature, oxygen, and labile organic matter decrease with depth, whereas pressure increases (Thistle 2003). Because each of the environmental factors that varies with depth can influence the settlement, survival, and growth of benthic organisms, it is not surprising that depth-related changes in the seamount biota are prominent.

Seamount habitats have diverse environmental conditions reflected in hydrodynamic regimes, substratum types, and deposition dynamics. Differences in seabed morphology influence hydrodynamic flow patterns and therefore the deposition of sediment and organic matter. For example, conical seamounts can have steep rocky surfaces swept by relatively fast currents, and creviced slopes with patches of soft sediment. In contrast, flat-topped guyots can have low relief and relatively quiescent summits covered with soft sediment, and steep slopes that are mostly bare rock. This in turn affects the distribution and abundance of benthic fauna; for example, corals and other filter feeders are clustered on elevated features where swifter currents prevail (e.g., Genin et al. 1986). Such patchiness can also be evident for soft-sediment infauna where there are differences in topographically induced currents and sediment coarseness (Levin & Thomas 1989). These sorts of observations have recently been confirmed by a detailed depth-related photographic study of

megafauna on contrasting seamounts off California (Lundsten et al. 2009). The distinctiveness of the depth-faunal assemblage pattern is related to elevation of the seamount and its relative position in the water column. If the summit extends into the photic zone, phytoplankton production may directly support a rich and diverse benthic fauna on the shallower regions. If a seamount penetrates into an oxygen-minimum zone (OMZ), the fauna can be sparse on the summit (where they are physiologically controlled) but more abundant on the slope below the OMZ (Wishner et al. 1990, Levin et al. 1991a).

Pratt (1967) showed that the type and characteristics of the substratum can control the benthos, with attached corals and sponges being restricted by the availability of hard substrata and few organisms occurring on manganese crusts. On three seamounts in the Gulf of Alaska, Raymore (1982) demonstrated the role that habitat diversity plays in controlling faunal diversity, finding the highest megafaunal diversity associated with the greatest variety of topography (and microrelief). Kaufmann et al. (1989) found that some taxa have random distributions while others are more patchily distributed at scales of 10–1000 m, possibly the result of random distribution of food resources, random foraging behavior, and/or current strength (related to rates of food supply and/or effects of increased sediment transport). Megaepifaunal assemblages on Great Meteor Seamount showed distributional patterns at the scale of 10 km, possibly due to topographically induced flow patterns that affected sedimentation rates, in turn influencing food supply, retention/accumulation of planktonic larvae, and seabed composition (Piepenburg & Müller 2004).

Infaunal assemblages on seamounts have not often been studied. Levin et al. (1994) found that two sedimentary sites on the summit of Fieberling Guyot differed in composition and explained this by the contrasting sediment transport regimes. Perhaps at the smallest spatial scale yet examined, Levin et al. (1986) showed changes in the meio- and macrofauna at scales of <15 cm that were related to sediment-agglutinating xenophyophores (giant protozoans), which may have altered local hydrodynamic conditions, increased particle flux of fine-grained material to the seabed, and provided associated fauna with a substratum, food, and refuge.

Like xenophyophores, corals and other large sessile organisms provide biogenic structure that influences associated fauna on seamounts. Matrix-forming stony corals, in particular, can provide structure on the scale of 1–1000 m. These living structures, and their broken skeletal remains (i.e., coral rubble) provide habitat that can locally increase benthic diversity (Henry & Roberts 2007) and contribute to larger scale differences in the composition of seamount assemblages (O'Hara et al. 2008). Biogenic structures are also associated with bioturbating fauna of soft sediments. These lebenspuren, such as feeding pits, burrow openings, mounds, trails, and fecal casts are typically centimeters to meters in dimension. Kaufman et al. (1989) found these features varied in abundance and distribution on a seamount. Bioturbation (via physical disturbance of sediment, nutrient recycling, etc.) likely influences seamount fauna as it does fauna elsewhere (Widdicombe et al. 2000).

Most seamounts are of volcanic origin and can support active hydrothermal venting. Venting creates unique physicochemical conditions with distinct benthic assemblages (e.g., chemosynthetic species, often with high biomass) that extend from centimeters to hundreds of meters (e.g., Tunnicliffe et al. 2003). The elevated productivity associated with venting also influences the composition and abundance of background assemblages (Van Dover 2000). Levin et al. (1991b) observed on eastern Pacific seamounts polychaete densities consistently lower at the hydrothermal field setting than elsewhere on the seamounts. Because of the dramatic nature of hydrothermal venting, its presence or absence will likely result in large-scale differences in faunal composition among seamounts (Limén et al. 2006).

Despite considerable advances in understanding the environmental drivers of the seamount benthos, specific relationships and interactions between drivers have not always been well resolved. Most data have come from observations, but experiments are required to test specific hypotheses

about faunal-environmental coupling. There are also some potentially important environmental drivers that have received little attention to date, such as submarine landsliding and explosive submarine eruptions (Kayen et al. 1989, Wright et al. 2008), the chemical properties of rock and sediment (e.g., Pratt 1967, Grigg et al. 1987), and discrete pulses of organic matter/debris (or flocs) to the seafloor (Reimers & Wakefield 1989).

(4) Biological Productivity of Seamounts

Seamounts are locations for a broad range of current-topography interactions and biophysical coupling, with implications for both phyto- and zooplankton. Seamounts appear to support relatively large planktonic and higher consumer biomass when compared to surrounding ocean waters, particularly in oligotrophic oceans. It has been a widely held view that in situ enhancement of primary production fuels this phenomenon, but this has recently been challenged (Genin & Dower 2007). Productivity in oceanic settings depends on light and nutrient availability, while overall production is the result of productivity and accumulation of the phytoplankton. At a seamount, either (a) a seamount-generated, vertical nutrient flux has to be shallow enough to reach the euphotic zone and the ensuing productivity retained over the seamount long enough to allow transfer to higher trophic levels, or (b) the seamount must rely on allochthonous inputs of organic material to provide a trophic subsidy to resident populations.

A classical view of the biophysical coupling leading to enhanced primary productivity is nutrient upwelling associated with the presence of a Taylor cone over a shallow seamount. Taylor cones form as a result of steady flow over a seamount, which may create both an anticyclonic flow and isopycnal doming over the seamount, bringing nutrient rich waters shallower. The vertical extent of Taylor cones is inversely proportional to the density stratification (White et al. 2007a). If the seamount summit is shallow enough, or vertical stratification is not too strong, doming may reach the euphotic zone. Additional nutrient fluxes to the euphotic zone may be achieved through enhanced turbulent mixing at the seamount, associated with internal waves and other baroclinic wave motions (Toole et al. 1997, Kunze & Stanford 1997).

Genin & Dower (2007), however, argue that observational evidence for such local augmentation of primary production at seamounts is inconclusive. While enhanced phytoplankton concentrations have been observed on seamounts such as Cobb (Dower et al. 1992), Great Meteor (Mouriño et al. 2001), and Minima-Kasuga (Genin & Boehlert 1985), long-lasting elevated levels of plankton over seamounts have not generally been recorded. A maximum retention time for high plankton concentrations of three weeks has been reported (Dower et al. 1992). Such short residence times for phytoplankton stocks will not allow substantial transfer to higher trophic levels, but the variability in the local seamount dynamics may instead shed plankton from the seamount downstream. Thus seamounts may provide significant downstream patchiness in plankton production and distribution.

The lack of retention of passive material at seamounts is a result of mesoscale variability in dynamic forcing (White et al. 2007a). Taylor cone generation and persistence is based on the stability of steady-forcing flow meeting certain criteria. The ocean has significant mesoscale variability, such as ocean eddies, internal tides, and variable meteorological forcing, and hence is likely to make any local seamount dynamic response both variable and complex. Surface forcing would be particularly important for shallow or intermediate-depth seamounts, where the seasonal thermocline would act to decouple local dynamics with the overlying near-surface layer (C. Mohn & M. White, unpublished paper).

Steady forcing, however, is not the only mechanism that can generate both anticyclonic flow and isopycnal doming. Tidal forcing, particularly at a period greater than the local inertial period

($2\pi/f$), may also generate rectified flow around the upper flanks of a seamount (Kunze & Stanford 1997). Tidally forced circulation may be a potent retention mechanism for intermediate or deep seamounts, especially near the level of the permanent thermocline where diurnal tides may be intensified at the seafloor (Brink 1995, White et al. 2007b). In addition, this can cause large organic matter fluxes through current acceleration and turbulent mixing, which is important for suspension-feeding benthic communities on deeper seamounts (e.g., Genin et al. 1986, Mienis et al. 2007).

This high retention potential of intermediate-depth seamounts may be important for the second mechanism—input of allochthonous fluxes of organic material (discussed above)—to enhance production at seamounts. Numerous studies have indicated the importance of seamount trapping of vertically migrating zooplankton (see review by Genin & Dower 2007), which occurs when zooplankton in the deep scattering layer rise to surface waters at night and a portion is advected by the surface flows over the seamount. The zooplankton are trapped at the seamount summit during the subsequent dawn descent and are then preyed on by fish or other planktivores. This mechanism may be a key trophic pathway to support the biological enrichment of pelagic (and subsequently benthic) seamount communities where in situ primary production alone would be insufficient.

Biophysical coupling, therefore, can have a profound effect on the production at seamounts. Localized dynamic responses may promote productivity through nutrient fluxes and also production through retention processes (Figure 2). Inherent variability in the dynamic forcing,

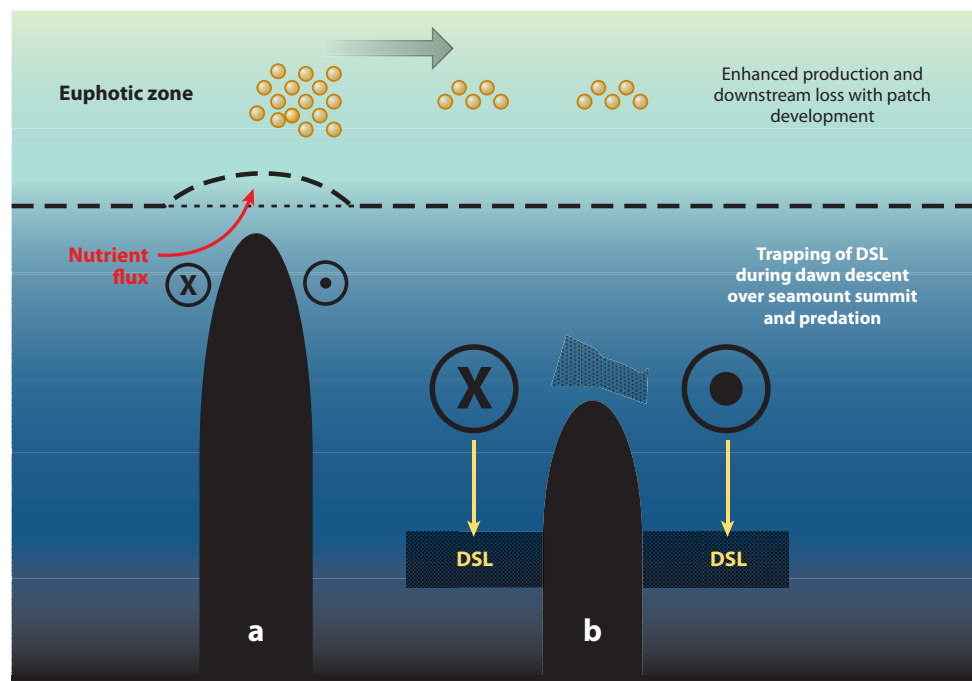


Figure 2

Schematic showing the processes contributing to organic matter fluxes at (a) shallow and (b) intermediate/deep seamounts. (a) Vertical nutrient fluxes promote surface primary productivity, which is lost due to weak retention over the seamount. (b) Seamount-trapped, vertically migrating zooplankton are preyed on by higher trophic levels. (Abbreviations: DSL, deep scattering layer; the circled X and black dot represent flow direction into, and out of, the plane of the page, respectively.)

particularly at shallow seamounts, can prevent plankton accumulation and contribute to mesoscale variability in the surrounding ocean. Tidally driven responses are thought to be more robust, especially at depths where mesoscale variability may be reduced or where tidally forced responses result in strong rectified flows and stronger currents. However, recent modeling studies (C. Mohn & M. White, unpublished paper) have indicated that variable forcing can sometimes retain passive organic material close to a seamount. Steady, and amplitude-modulated, inflow generated a downstream particle loss, but changes in the inflow direction caused some limited aggregation of tracers in the immediate vicinity of the summit. Such variability over relatively short time- and space scales, in an already variable ocean, limits interpretation of one-off or local field surveys. Future research will need to synthesize process models, include a full range of physical forcing characteristics, and validate results with long-term monitoring programs at key seamount sites. Research that examines the nature and control of benthic production, and the extent and mechanisms of coupling between pelagic and benthic productivity, will also be required.

(5) Seamount Trophic Architecture

Biological production on seamounts is often manifested in dense aggregations of benthopelagic and demersal fish that represent concentrations of high biomass for these species (Koslow 1997, Koslow et al. 2000). It is also thought that the biomass of benthic consumers on seamounts is elevated (e.g., Rogers 1994), but there are no studies that provide specific evidence of this. Three energetic processes have been proposed to support the large biomass of seamount consumers (reviewed by Genin 2004, Genin & Dower 2007) (see section 4): (a) phytoplankton production: the classical view that enhanced primary production on seamounts fuels higher-order predators through bottom-up subsidy of consumer biomass; (b) topographic trapping: summits and flanks of seamounts can block the descent of vertically migrating zooplankters, which are intercepted and preyed on by seamount consumers; and (c) trophic subsidy: when flow regimes impinge with seamount topographies, the accelerated currents amplify the horizontal food supply to seamount communities.

Filter feeders, such as sponges, corals, and crinoids, generally dominate the benthic invertebrate assemblages (Samadi et al. 2007). This observation suggests that benthic food chains are short and that their structure is simple. While there are very few trophic studies for seamounts, findings to date indicate that benthic food webs on seamounts display a diverse trophic architecture that in terms of food-chain length rivals that of other marine communities, both shallow and deep (Samadi et al. 2007). Trophic diversity in the benthos arises from evolutionary differentiation of feeding modes among higher taxa that range from deposit feeders (e.g., holothurians) to predators (e.g., asteroids). Feeding flexibility is also instrumental in enhancing trophic heterogeneity; for example, sponges are highly efficient at capturing ultraplankton (Pile & Young 2006) but also include carnivorous forms that prey on copepods (Watling 2007).

Intense grazing pressure on zooplankton over seamounts (Haury et al. 1995) indicates their important role in the transfer of energy within the seamount food web. Major predators of zooplankton are midwater fish, which probably form an important trophic link to higher predators, including squids, piscivorous fishes, seabirds, and marine mammals (Morato et al. 2008). Midwater fish include micronektivores feeding primarily on shrimps and/or cephalopods (Porteiro & Sutton 2007, Pusch et al. 2004, Sutton & Hopkins 1996). Pelagic prey is also the main energy supply for many benthopelagic and demersal fish (Porteiro & Sutton 2007), and modeling indicates that advection of mesopelagic fish and crustaceans is necessary to support aggregations of fish such as orange roughy and oreostomatids on seamounts (Williams & Koslow 1997, Bulman 2002). Thus, pelagic food webs associated with seamounts play pivotal roles in channeling energy

to fish species and attracting top pelagic predators to seamounts (Haury et al. 1995, Morato et al. 2008).

High-productivity seamount ecosystems operate via a trophic architecture composed of diverse pelagic and benthic consumers whose biomass is often elevated compared with the surrounding ocean. Energetic subsidies that operate via trapping of migrating zooplankton and interception of horizontally advected micronekton are much more likely to underpin food webs on most seamounts (Genin & Dower 2007, Morato et al. 2009) than is localized enhancement of plankton production that propagates to higher consumers in a classic bottom-up mechanism (see section 4). Thus, food webs are probably supported largely by imports of allochthonous material, making seamounts spatially subsidized systems (sensu Polis et al. 1997) where cross-boundary fluxes of matter and energy are the pivotal processes at the base of food webs.

In conclusion, it appears that the trophic architecture for seamounts has a relatively unique character, comprising a diverse array of consumers, loosely coupled pelagic and benthic components, and multiple bases for the food web, all of which can be influenced by topographic and oceanographic driving forces. These combine in ways that can support high biological production. However, few detailed trophic studies have been conducted for seamounts (particularly those that involve isotopic investigative tools) and future research is required to advance our general understanding.

(6) The Vulnerability of Seamounts to Human Activities

Biological communities on seamounts face a number of threats from human activities. The most widely known of these is fishing, especially trawling, although in recent years the potential has increased for exploitation of mineral resources.

Historically, seamounts have supported fisheries for pelagic tunas, mackerels, and smaller-scale line fisheries (e.g., black scabbardfish *Aphanopus carbo*) for many decades (da Silva & Pinho 2007), but in the 1970s, extensive trawling began on seamounts as fleets discovered large aggregations associated with them. There are now major seamount fisheries for alfonsino (*Beryx splendens*), pelagic (slender) armorhead (*Pseudopentaceros wheeleri*), black cardinalfish (*Epigonus telescopus*), orange roughy (*Hoplostethus atlanticus*), roundnose grenadier (*Coryphaenoides rupestris*), oreos (smooth oreo *Pseudocyttus maculatus*, black oreo *Alloctytus niger*), and toothfish (*Dissostichus eleginoides*, *D. antarcticus*) (e.g., Morato & Clark 2007, Clark et al. 2007).

At least 2 million metric tons of deep-sea species are known to have been trawled from seamounts since the late 1960s (Clark et al. 2007), although much has not been officially reported and therefore the United Nation's Food and Agriculture Organization (FAO) statistics give lower estimates (Watson et al. 2007). The main fisheries have been for pelagic armorhead and alfonsino on the Hawaiian and Emperor seamount chains in the Pacific Ocean. Orange roughy, oreos, and alfonsino continue to support locally important fisheries in the SW Pacific. Orange roughy have been targeted on seamounts worldwide, with roundnose grenadier being a major seamount fishery in the North Atlantic. Smaller fisheries for alfonsino, mackerel, and cardinalfish have occurred in the Mid-Atlantic, SE Pacific, SW Indian Ocean, and off the west coast of North Africa. In the Southern Ocean, fisheries for toothfish, notothenids, and icefish can occur on seamounts (Clark et al. 2007).

Few of these large-scale seamount trawl fisheries have proved sustainable, with many showing a boom-and-bust pattern (e.g., Uchida & Tagami 1984, Vinnichenko 2002). Sissenwine & Mace (2007) listed 44 area-species combinations globally, and 27 of these included stocks classed as overexploited or depleted. Many deep-sea commercial species have characteristics that generally make them more vulnerable to fishing pressure than shallower shelf species. They can form large



Figure 3

Large catches can still be taken on seamounts, but only if effort and overall catch levels are tightly controlled. This shows a catch of about 50 metric tons of orange roughy taken off New Zealand (Photo: NIWA).

and stable aggregations over seamounts for spawning or feeding, which enables very large catches (**Figure 3**) and rapid depletion of stock size. Biological factors such as longevity, low fecundity, and slow growth rates make recovery from fishing impacts slow (e.g., Clark 2001, Morato et al. 2008). Seamount fisheries have typically proven difficult to research and manage sustainably (e.g., Francis & Clark 2005, Morato & Pitcher 2008). Once overexploited, it is uncertain if deep-sea fisheries on seamounts can recover, and irregular recruitment levels may be a key factor (Clark 2001, Dunn 2007). Successful seamount fisheries today are typically low-volume and based on high-value species (Clark 2009). The low effort and catch levels in current trawl fisheries may make them more sustainable, similar to small catches of a number of artisanal seamount fisheries that have existed for centuries. About a quarter million metric tons of fish are caught annually in hook-based fisheries (handline, and pole and line) conducted from small boats in Madeira, Hawaii, and the Azores, Seychelles, and Pacific Islands (Marques da Silva & Pinho 2007).

There have been numerous advances in fishing technology that have enabled extensive bottom trawling on seamounts. Ground gear now features large bobbins and discs to roll over the rough seafloor that previously would have snagged and damaged lighter gear and nets. Advances in navigation and electronic technology (e.g., GPS, echosounders, sonars, net sensors, automatic winch control) mean that vessels can easily locate a seamount, find fish aggregations, and trawl repeatedly (Clark & Koslow 2007). The catch of orange roughy taken from seamounts rose from 20 to over 70% of the total New Zealand orange roughy catch between the 1980s and mid-1990s (Clark & O'Driscoll 2003). As with catch, effort levels on seamounts can also be very high. Soviet

fishing effort for pelagic armorhead on North Pacific seamounts was about 18,000 trawler days between 1969 and 1975 (Borets 1975). Hundreds to thousands of trawls have been carried out on small seamounts in the SW Pacific, and O'Driscoll & Clark (2005) estimated a median total trawl distance on New Zealand seamounts of 130 km per square kilometer of seamount area. The bottom impact of trawling on seamounts can therefore be much greater and more concentrated than for slope fisheries where effort is spread out over larger areas.

Many bottom fishing operations can have serious physical and biological impacts on seamount habitats and communities, but bottom trawling is the most damaging (see review by Clark & Koslow 2007). There are direct impacts on benthic communities caused by physical disturbance from the trawl but also indirect effects through selective removal of particular species and sediment resuspension and mixing that can change the structure of the habitat and alter community composition. There have been few research studies on deepwater fishing impacts (see review by Gage et al. 2005), but studies on seamounts off Australia and New Zealand have demonstrated differences in the structural complexity of benthic habitats, species numbers and abundance, and overall community composition and structure between fished and unfished/lightly fished seamounts (Koslow et al. 2001, Clark & Rowden 2009). Sessile fauna, such as sponges, echinoids, and corals, are particularly vulnerable to damage because they can be large, fragile, and long-lived (Probert et al. 1997).

Although fishing has generally been the main human activity on seamounts, the potential for mining to impact seamount habitats and biological communities is increasing. The deep sea is of interest for oil and gas exploration, to sequester carbon dioxide, and for mining manganese nodules, cobalt-rich crusts, and polymetallic sulfides (e.g., Glover & Smith 2003, Davies et al. 2007). Seamounts can have thick deposits of cobalt-rich ferromanganese crusts (Hein 2002), especially in the Pacific Ocean (e.g., around Hawaii, Micronesia, Marshall Islands), and technology is developing to enable recovery of such deposits (Sharma 2007). Precious metals are deposited at sites of hydrothermal activity (Scott 2007), and polymetallic sulfide deposits are of current commercial interest in the SW Pacific (e.g., Papua New Guinea, New Zealand, Vanuatu). The effects of mining are uncertain because so few studies have been carried out, but direct physical disturbance and sediment plumes (e.g., Amann 1993, Van Dover 2007) would be similar to, and potentially greater than, trawling effects. Careful controls will be needed to restrict the impact on benthic fauna (e.g., Baker et al. 2001, Glover & Smith 2003, Shank 2009) of seamounts, especially those with vent communities that may be geographically isolated.

Whether from fishing or mining, biological communities on seamounts are highly vulnerable to human activities. The small area of many seamounts, the concentration of both resources (fish aggregations, high mineral densities), and exploitation (e.g., numerous trawls) mean that human impact can be more severe than in habitats such as the continental slope where communities and human activities are more dispersed.

(7) The Resilience of Seamount Communities to Human-Induced Disturbance

Several aspects of resilience are useful in considering human-induced disturbances of seamount habitats and fauna: (a) amount of disturbance the ecosystem can withstand without changing self-organized processes and structure (Holling 1973, Gunderson 2000); (b) speed of recovery following disturbance (Hall 1994); (c) possibility of multiple stable states along a recovery trajectory (Knowlton 2004); (d) nested spatial scales that stable states may occupy (Peterson et al. 1998); (e) reduced resilience of communities adapted to lower natural environmental disturbances (Jennings & Kaiser 1998); and (f) changes occurring with natural episodic "disturbance" over longer timescales (e.g., Wright et al. 2008).

Table 1 Examples of age estimates of seamount invertebrate megabenthos

Faunal group	Age (years)	Method	Reference
Glass sponge	440	Ring count	Samadi et al. 2007
Stalked crinoid	340	¹⁴ C dating	Samadi et al. 2007
Zoanthid (<i>Gerardia</i> spp.)	400–900	¹⁴ C dating	Roark et al. 2006
Zoanthid (<i>Gerardia</i> spp.)	1800	¹⁴ C dating and ring count	Rogers et al. 2007
Gorgonian coral	67–2377	¹⁴ C dating	Roark et al. 2006
Bamboo coral	35–197	¹⁴ C and ¹²⁰ Pb dating	Rogers et al. 2007
Biogenic habitat (accumulated)	1000–50,000	U/Th dating	Rogers et al. 2007

Only a few studies have examined impacts of fishing on the benthic communities of seamounts. Koslow et al. (2001), Clark & O’Driscoll (2003), and Clark & Rowden (2009) inferred cause-and-effect of trawling by comparing areas subject to different intensities of disturbance (from untrawled to heavily trawled), while Althaus et al. (2009) examined seamounts in quantitative repeat surveys. In contrast, there are many studies of fishing impacts in shallow continental-shelf environments that have demonstrated recovery (of species richness, abundance, population biomass and production) can take several years and is dependent on both the type and extent of impact and the natural levels of disturbance that characterize a community (see reviews by Collie et al. 2000, Kaiser et al. 2006, Pitcher et al. 2008). Many seamount taxa are extremely long-lived and grow very slowly, especially those forming biogenic habitats (some scleractinian corals) and those adding structural complexity (e.g., large erect anthipatharian and gorgonian corals, sponges, and crinoids) (**Table 1**). Some of these low-productivity components of benthic ecosystems on seamounts can therefore be expected to have less capacity to absorb human disturbance and take much longer to recover than their shallower, more productive counterparts.

Habitat type is a key determinant of recovery rate of the benthos in shallow environments, with those that are associated with biogenic structures the slowest to recover (Collie et al. 2000, Kaiser et al. 2006). Deep biogenic habitats can be major components of benthic community composition on seamounts where patchy thickets of framework-building scleractinian corals can provide interstices for a diverse mobile fauna (O’Hara et al. 2008) and attachment sites for a great variety of sessile filter feeders (Rogers et al. 2007). These biogenic habitats may accumulate over geological time (many millennia) (**Table 1**) but can be rapidly reduced by bottom trawling (e.g., Koslow et al. 2001, Clark & Rowden 2009). On an Australian seamount that had been heavily trawled, structure-forming taxa showed no signs of recolonization 10 years after trawling had ceased (Althaus et al. 2009). However, this study, as well as repeated surveys on New Zealand seamounts (M.R. Clark, unpublished data), also found some species that were more abundant on trawled rather than unfished seamounts. Their ecological traits (**Table 2**) indicate potential for rapid or local-scale recolonization or resistance to direct physical impacts (**Figure 4**). Repeat surveys also found isolated patches of diverse fauna, including coral-associated communities in natural refuges (i.e., very rough areas) inaccessible to trawls. Benthic communities in impacted seamount areas are a mix of early recolonizing species (e.g., stylasterid corals), possibly including some that respond positively to trawling as competition for living space or food is reduced, and others that survived the direct impact of trawling (e.g., gold corals).

The relative rates and sources of recruitment and immigration of benthic species to disturbed areas are highly uncertain because of variation in suitable settlement substrate on and between individual seamounts, irrespective of trawling history (Althaus et al. 2009). This variation can be expected to be greater on larger, more topographically complex seamounts than on

Table 2 Examples of megabenthic taxa on seamounts that appear more resilient to trawling impacts

Taxon	Ecological traits and observations
Hydrocorals: <i>Stylaster</i> sp. ^a <i>Calyptopora reticulata</i> ^b <i>Lepidotheca fascicularis</i> ^b	Small size ($\lesssim 100$ mm height) ^{a,b} ; many (most) species brood with possibly continuous or protracted spawning; possibly short-lived larvae; most slow growing ^d , but some (emergent) species fast growing ^e ; ubiquitous in survey areas ^{a,b}
Gold corals: <i>Chrysogorgia</i> spp. ^{a,f}	Small size ($\lesssim 200$ mm height), compact (bottle-brush), and flexible ^c
Chrysogordidae (undescribed species) ^a	Small size ($\lesssim 300$ mm height), whiplike, robustly stiff but flexible ^c ; abundant on heavily fished seamount in 1997 and 2007 surveys ^c
Bryozoan: <i>Lagenipora</i> sp. ^b	Small encruster considered opportunistic in disturbed environments ^b
Anemone: ?Actinernidae ^c	Anemones have capacity for local-scale mass colonization by larvae or brooded juveniles; not colony forming but have propensity for clustered distributions in shallow water ^f ; on a single heavily trawled seamount, uncommon in 1993 but highly abundant in 2008 ^c

^aF. Althaus, A. Williams, T.A. Schlacher, R.J. Kloser, M.A. Green, unpubl. paper; ^bClark & Rowden 2009; ^cA. Williams (CSIRO), unpubl. data; ^dBrooke & Stone 2007; ^eMiller et al. 2003; ^fK. Gowlett-Holmes (CSIRO), pers. commun.

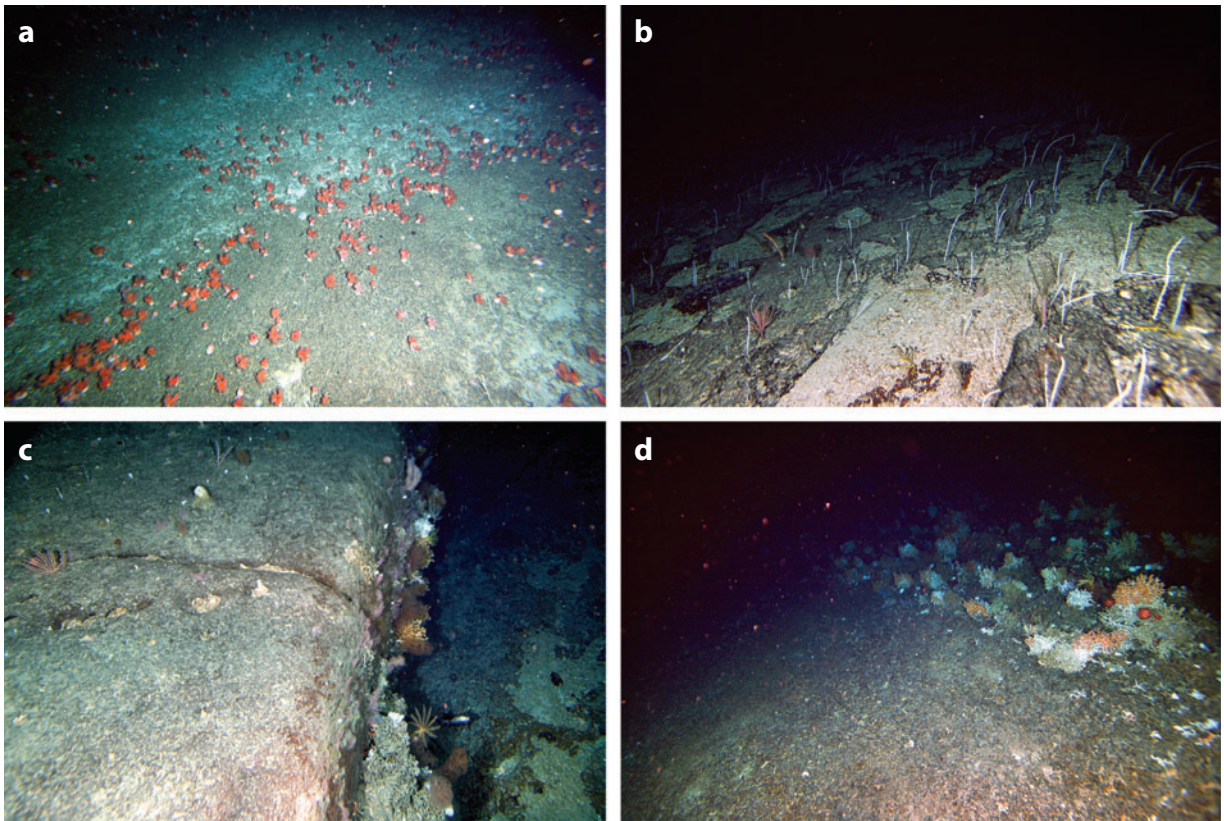


Figure 4

Photographs from southeastern Australian seamounts showing (a) apparent early colonization by an anemone (Fam. ?Actinernidae) at 800 m depth on the heavily fished St. Helens Seamount three years after fishing ceased; (b) the small whiplike, stiff but flexible, gold coral (undescribed species of Fam. Chrysogordidae) at 1118 m depth on the heavily trawled Pedra Seamount; (c) rock overhang providing a natural refuge at 1183 m depth on the heavily trawled Mongrel Seamount; (d) sharp interface showing apparent removal of stony coral and associated megafauna from passage of single trawl at 1338 m depth on lightly fished Dory Hill.

small conical features. Natural patterns of connectivity between seamounts are also variable (see section 2). Many seamount species are nonplanktotrophic (Parker & Tunnicliffe 1994), indicating that dispersal beyond closely spaced seamounts may be limited or slow. Althaus et al. (2009) found no evidence of widespread recruitment from external sources, indicating that initial recovery may occur only in small patches.

Based on the limited number of seamount studies and the knowledge gained by research from shallower shelf and slope areas, it is likely that recovery trajectories for benthic communities on seamounts will span decades or centuries, especially for widely separated seamounts. Stable states of recovery have not yet been recognized, it is uncertain whether systems will recover to their original ecological structure, and the effects of episodic natural disturbance are unknown. There is clearly a need for further research to adequately determine the resilience of seamount habitats to human-induced disturbance, but at present it is reasonable to consider the biological communities of seamounts to be among the least resilient in the marine environment.

(8) Balancing Exploitation and Conservation of Seamounts

The characteristics of deep-sea ecosystems present a different set of conservation challenges from shallow-water ecosystems (Glover & Smith 2003) and the scientific basis necessary for the successful management, protection, and restoration of deep-sea habitats such as seamounts is limited at national and international levels (Davies et al. 2007). However, with issues of deep-sea conservation being considered at the level of the United Nations General Assembly in 2007 and 2008, science has to provide information to help guide the conservation and sustainable management of seamounts.

There is extensive legislation and a variety of management tools that can be applied to seamounts (e.g., Probert 1999, Alder & Wood 2004, Molenaar 2007, Probert et al. 2007). Broadly speaking, seamount conservation strategies may be apportioned into activity-specific measures (short-term) and site-specific measures (long-term), with seamounts being regarded as appropriate for the latter (Gubbay 2005). Most countries have a variety of legislative options (e.g., under fisheries, minerals, transport and navigation, protected areas legislation) that can be used to manage seamounts. Hence the instruments to protect seamounts exist (e.g., MPAs, closed areas, site-based effort control, licensing, gear restrictions) but examples of their implementation are rare (Alder & Wood 2004, Probert et al. 2007). Of an estimated 155 countries that contain seamounts within their maritime jurisdictions, in 2004 only 22 had legislature in place to protect all or a portion of seamounts (Alder & Wood 2004), although that has probably increased in recent years (Anon. 2008).

Despite numerous calls for high-seas seamount management, there is no unified, single managing authority or mechanism in place that can provide fully for the management/protection of seamounts from the most pressing threat, fishing. Regional fisheries management organizations provide the best option for seamount protection, and although there are 12 of these (with several more developing), there are gaps in global coverage and inconsistent measures to prevent damage or destruction to vulnerable habitats like seamounts. Recent FAO guidelines (Rogers et al. 2008, FAO 2009) should increase effective management of biological communities on seamounts. The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) is one of the agreements that extends past fisheries-only management and employs highly precautionary, ecosystem-based management. CCAMLR is implementing a system to identify vulnerable marine ecosystems, such as cold-water coral and sponge communities, when encountered by fishing operations and to protect them when reported. They are also developing a network of MPAs across the Southern Ocean/Antarctic region.

Just as potential threats to seamounts can vary in scale, so too can physical characteristics (see section 3) and biological communities of seamounts (see section 1). Thus, no single management model can be applicable to all seamounts. Management strategies must incorporate natural variability over time and space, crossing major jurisdictional divisions to ultimately feed into a larger regional or global framework (Probert et al. 2007).

An increase in basic ecological research is crucial to assist the design of marine reserves and networks. However, limitations to knowledge or data should not restrict efforts toward seamount conservation. A useful first step is the development of biologically meaningful seamount description/classification schemes (Stocks et al. 2004); one such classification exists for the seamounts of New Zealand (Rowden et al. 2005). Increasingly, predictive modeling of species distributions and/or suitable habitat that extrapolate from better-known areas will offer information about data-poor areas (e.g., Tittensor et al. 2009). Classifications and species/habitat models can be used, together with selection tools, to design a network of MPAs that can provide protection for benthic communities while allowing access to areas for resource exploitation (e.g., Leathwick et al. 2008). However, MPA success in the deep sea is largely untested, and researchers need opportunities to study these communities to inform future management strategies (Alder & Wood 2004).

As society strives to reconcile human exploitation and conservation, it is clear that balancing economic and ecological considerations is not a simple task. For example, biologically sustainable deep-sea fish catches could prove uneconomical (Davies et al. 2007). Options to manage fisheries versus those for benthic conservation (e.g., Rogers et al. 2008) may conflict over decisions to continue exploiting already fished seamounts while closing unfished regions. The ultimate success of seamount management relies on open dialogue and free exchange of information between all seamount stakeholders. Management organizations and state governments must work with resource users to support scientists in addressing information gaps to better inform approaches to seamount management (Probert et al. 2007).

THE FUTURE

Seamount research has progressed substantially over the last decades. However, despite the increased geological, oceanographic, and biological sampling of seamounts, data are only available from a small percentage of the oceans' seamounts. Future research can best build upon the existing knowledge by strategically targeting understudied regions, types of seamounts, and critical ecological processes; by employing new sampling and analysis technologies; by using modeling approaches to extrapolate from the known to the unknown; and by standardizing data collection and sharing.

Some seamount types and locations are understudied, including deep seamounts, and those at high-latitudes and in equatorial regions, particularly in the Indian Ocean, southern Atlantic Ocean, and western and southern central Pacific Ocean (**Figure 5**). The summits of seamounts are much more intensively sampled, especially on deep seamounts (Stocks 2009). What little work has been done on the deep slopes and bases of seamounts, however, indicates that these support distinct assemblages (e.g., Baco 2007). Some of this uneven sampling effort is due to technical limitations; seamounts deeper than ~2000 m cannot be easily sampled by trawls and require specialized gear such as remotely operated vehicles (ROVs) or submersibles.

Biological sampling also has some taxonomic bias, especially toward larger animals such as fishes, crustaceans, and corals; these are the most commonly reported groups in SeamountsOnline (Stocks 2009). Other macrofaunal groups and the meiofauna are less well covered, and many of the smaller organisms are identified at higher taxonomic levels only (but see Gad 2004, Gofas

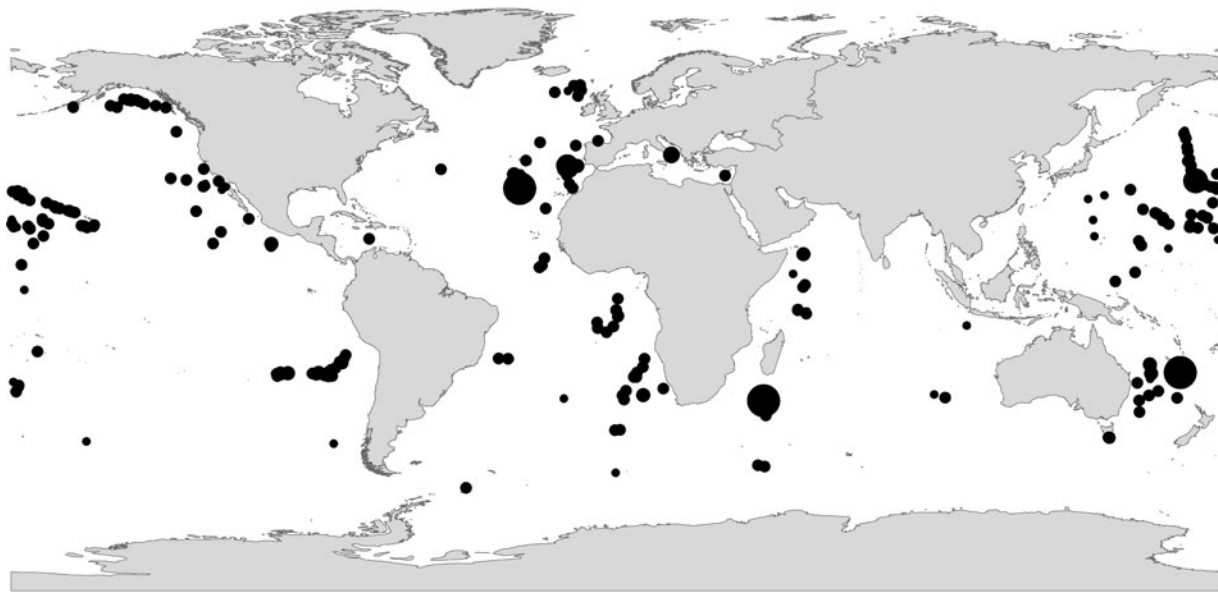


Figure 5

Seamounts for which SeamountsOnline (<http://seamounts.sdsc.edu>) has species occurrence information. Circle size is proportional to the number of species records, a proxy for sampling intensity, with sizes scaling from 1 to 1500 records. CenSeam has identified priority regions for future research due to undersampling: Indian Ocean, western and southern central Pacific, and southern Atlantic.

& Beu 2002). The microbial communities of seamounts without hydrothermal vents are virtually unknown. New methods, such as barcoding and metagenomics, may make inventories of taxonomically difficult organisms more tractable, but the restricted number of trained taxonomic experts will remain a major limiting factor.

Seamount sampling to date has focused largely on species inventories, and in fewer instances, on documenting the structure of whole assemblages. These latter programs have been instrumental in shaping and advancing our understanding of seamount ecology. In the future, process-oriented studies (e.g., OASIS, <http://www1.uni-hamburg.de/OASIS/>) and genetic and functional approaches will be important complements. For example, one of the key questions about seamounts is to what degree they act as isolated habitats that can give rise to potentially endemic species and distinct communities (see section 1) and should thus be managed as discrete habitats. Genetic techniques can indicate the levels of population isolation on seamounts, and cross-disciplinary studies comparing the hydrography of individual seamounts to larval characteristics can predict potential connectivity (see section 2). Recent advances in ocean-observing technologies, such as moored instrument arrays and gliders, make long-term observation on seamounts possible. Such time-series sampling is likely to provide new insights into temporally variable processes, such as the dynamics of Taylor cones and their effects on productivity and plankton distribution (see section 4).

The many seamounts in the world's oceans make it impossible to biologically survey even a good proportion of them adequately. Hence, predictive modeling is a useful tool to enable an expansion of the spatial coverage of ecological information as well as develop hypotheses to direct future sampling. The recent work of Clark et al. (2006) and Tittensor et al. (2009) provides an example of habitat suitability modeling capable of predicting which understudied regions are most likely to have seamounts supporting cold-water corals in fishable depths.

Greater uniformity in collection methods, data processing, and data sharing has substantial potential for advancing seamount knowledge. To date, the large variety of sampling approaches, combined with a lack of good documentation and variable taxonomic attention, has meant limited data to support robust studies of large-scale biogeographic patterns on seamounts or to compare seamount to nonseamount habitats. Where possible, standard protocols for sample collection and processing should be developed and adopted. Complete biological data sets from expeditions should be contributed to global databases such as CenSeam's data repository, SeamountsOnline (Stocks 2009), and the Ocean Biogeographic Information System (<http://www.iobis.org>), with geological data feeding the Seamount Catalog (<http://earthref.org>).

In conclusion, future seamount research should target current gaps in geographic and bathymetric coverage, explore relatively undersampled habitats (e.g., deep slopes and bases) and communities (e.g., plankton, meiofauna, microbes), and use a combination of molecular tools and traditional taxonomy to produce high-quality and comparable biodiversity inventories and connectivity metrics. Major advances in our understanding of seamounts will emerge from increased multidisciplinary studies that operate across levels of biological organization—from genes to whole ecosystems—and that merge physicochemical processes with structural and functional aspects of seamounts within the deep-sea environment. Science will then be in a much stronger position to inform global seamount management and conservation.

SUMMARY POINTS

1. Seamounts can host diverse and abundant benthic communities, but in many cases the composition is broadly similar to that of adjacent continental slope. Several studies have suggested high levels of endemism on seamounts, but this assertion is problematic because of limited sampling. The prevailing concept of “islands in the sea” is not well supported.
2. Connectivity levels between seamounts vary considerably. Some taxa have limited dispersal capabilities and hence localized distributions. Others can disperse hundreds to thousands of kilometers and occur on widely separated seamounts.
3. Environmental drivers of biological communities on seamounts are not well known. Depth and substrate type are key elements in determining the composition and distribution of benthic fauna. Biogenic structures (e.g., coral, sponges) are also important for their associated communities.
4. Seamounts support aggregations of higher consumers (e.g., fish), but enhanced in situ primary production and a bottom-up process does not appear to be common. The enhanced production is probably due to the transfer and trapping of zooplankton from beyond the seamount itself and to interception of horizontally advected particles produced away from the seamount.
5. Seamounts have a diverse trophic architecture that is no simpler than that of other marine communities despite the dominance of filter feeders in the benthos. Complex topographic and oceanographic patterns may cause food-web structures to be variable.
6. Benthic biological communities on seamounts are highly vulnerable to human activities, especially fishing. Many benthic species are long-lived and slow-growing, and not resilient to human impacts. Management of fishing or mining must consider habitat conservation, and a network of MPAs is one option to achieve a balance.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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