



Seamounts: identity crisis or split personality?

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ABSTRACT

At present, researchers propose that over 14,000 seamounts exist and, like their terrestrial analogues, function like islands. In addition, seamounts are described as oases, biodiversity hotspots, and lush coral/sponge gardens. Here I discuss the extent to which these tenets regarding seamounts may be inappropriate, suffer from a lack of support, and be over-generalizations of a broad range of environmental types encountered on seamounts. Ultimately, for seamount science to progress, we need to challenge our conventional wisdom on these habitats and the extent to which all seamounts function in a similar manner.

Keywords

Biodiversity, conservation, coral, deep sea, ecological oasis, endemism, hotspot, island biogeography, isolation, seamount.

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INTRODUCTION

There is no such things as mountains and valleys on the deep-sea bottom.

Mosely (1880), p. 343

Less than 100 years after Mosely's statement, Hubbs (1959) contemplated the 'scientific interests, particularly in respect to zoogeography and speciation' of recently discovered submerged mountains in the Pacific Ocean. Approximately 14,000 seamounts, undersea mountains peaking below sea level (Wessel, 2001; Kitchingman & Lai, 2004), rise up from the ocean bottom. Like terrestrial mountains (Brown, 1971), seamounts seem an obvious system for the application of island biogeography and, to a large extent, the discourse on seamounts addresses issues of isolation, larval retention and endemism. For example, seamount literature often contains quotes such as '...the seamounts in clusters or along ridge systems function as "island groups" or "chains" leading to highly localized species distributions and apparent speciation...' (De Forges *et al.*, 2000); or 'Seamounts represent biological islands in the deep sea and often feature characteristic faunas that are quite different from those in the surrounding soft sediment and abyssal habitats' (Moore *et al.*, 2001). Conservation and policy also place seamounts in an island context. For example, in their contribution to the 2003 Defying Ocean's End Conference, Stone *et al.* (2003) claim that 'seamounts are rich and unusual deep-sea

biological communities that support highly unique and endemic faunas'. In 'Toward a strategy for high seas marine protected areas', Gjerde & Breide (2003) notes that 'Seamounts are areas of high endemic biodiversity with little overlap in community composition between seamount clusters'.

Alternatively, others suggest that seamounts are unique habitats for reasons not related to their 'islandness'. Seamounts may represent 'oases', where high carbon input increases standing benthic biomass, which in turn yields increased species richness (Samadi *et al.*, 2006). Biodiversity may also be elevated on seamounts because they possess dense coral and sponge meadows, providing habitat for a variety of organisms (Roberts, 2002). The distinctiveness of seamounts may also reflect the observation that they regularly contain hard-substrate habitats, for example rock outcrops, contrasting with the background soft-sediment that dominates a majority of the deep sea (Rogers, 1994). Yet many seamounts lack coral/sponge meadows or rock outcrops, possessing simply shallower soft-sediment communities than the deeper abyssal plain.

Certainly, seamounts are often idiosyncratic habitats that differ from the background deep-sea ecosystem. Here, I ask whether seamounts function ecologically or evolutionarily as islands, oases, biodiversity hotspots or reefs, or whether they are something wholly different.

WHAT ARE SEAMOUNTS?

Are seamounts islands?

By definition, an island (MacArthur & Wilson, 1967) is isolated such that gene exchange between two populations is obstructed (Whittaker & Fernández-Palacios, 2007). On the recent discovery of several submerged Pacific mountains, Hubbs (1959) asked 'To what degree has isolation on the banks and seamounts led to speciation?' Isolation is determined by the presence of a dispersal barrier (e.g. inhospitable habitat), distance between hospitable habitats, and the dispersal abilities of the species.

In itself, the deep ocean is not an obstruction to dispersal for seamount organisms. Other barriers must be present to generate isolation. Vermeij (2004) notes that, even for shallow marine organisms, 'deep ocean basins offer at most a porous barrier'. A prospective barrier is the potential for hydrographic conditions (e.g. seamount-trapped waves, tidal rectification or Taylor columns) to retain larvae on seamounts (Rogers, 1994). Of these potential hydrographic barriers, significant attention is given to Taylor columns (Rogers, 1994; De Forges *et al.*, 2000), which are anticyclonic eddies above the summit induced by currents encountering the seamount (Rogers, 1994; Genin, 2004). Little empirical evidence exists for the actual occurrence of Taylor columns (Vastano & Warren, 1976; Genin, 2004). On the few seamounts where physical oceanographic data are consistent with the presence of a Taylor column, they are often ephemeral, lasting less than 2 days to 6 weeks (Richardson, 1980; Genin & Boehlert, 1985; Comeau *et al.*, 1995). Tests of larval retention on seamounts (Rogers, 1994) due to Taylor columns or other flow mechanisms fail to document a statistically significant increase in larval numbers off or on the seamount (e.g. Mullineaux & Mills, 1998). If hydrographic conditions do serve as a dispersal barrier on some seamounts, it is likely this is a generalized phenomenon. [Correction added after online publication November 2007: The previous sentence should read: If hydrographic conditions do serve as a dispersal barrier on some seamounts, it is likely this is not a generalizable phenomenon.] Roden (1987) discusses a multitude of factors, flow velocity, stratification, varying Coriolis force over latitude, seamount size, and precise topography and the spacing, that interact on local to planetary scales to generate the complex and diversity of flows around seamounts.

Distance to a habitat of comparable depth or of similar habitat type could potentially also serve as an isolating mechanism (Rogers, 1994; Etter & Mullineaux, 2001). Under this hypothesis, each seamount experiences a relatively unique degree of isolation determined by the distances to similar habitats, or depths. A seamount, by definition, contains shallower depths than the surrounding environment. Deep-sea organisms show a considerable amount of zonation over depth (Rex, 1977; Gage & Tyler, 1982; Cartes & Carrasson, 2004), suggesting that species have distinct ranges limited by a combination of factors varying with depth (oxygen, temper-

ature, food availability and pressure). Seamounts also possess a variety of habitats including hard substrate walls, ledges and ridges; vents and seeps; oxygen minimum zones; and dense coral/sponge communities (Wishner *et al.*, 1990; Rogers, 1994; Auster *et al.*, 2005) contrasting with the surrounding soft-bottom seafloor (Auster *et al.*, 2005). Current research indicates that some deep-sea organisms show an affinity for these habitats (Roberts & Hirshvield, 2004). Yet none of these habitats is specific to seamounts, as they also occur on continental slopes (Etnoyer & Morgan, 2003, 2005). Thus distance to a suitable habitat is likely to be an isolating mechanism only in seamounts far from continental margins, for example those located in the Mercator Basin, a relatively flat area in the middle of the North Pacific.

Distance does appear as important for seamount communities as it is for any biological system (Nekola & White, 1999). Gastropod communities on seamounts off Brazil are more similar the more proximate they are (Leal & Bouchet, 1991), comparable to the macro- and megafauna patterns seen on seamounts in the South Pacific (De Forges *et al.*, 2000). However, the latter study is confounded by various sampling depths among the seamounts potentially leading to an underestimation of similarity. Large ranges also exist for species inhabiting continuous seamount chains and ridges (Wilson & Kaufmann, 1987). Connections via currents between seamounts can provide increased connectivity. Specific knowledge of currents along the Walvis Ridge, for instance, can predict the occurrence of the rock lobster, *Jasus tristani*, on the Vema Seamount (Lutjeharms & Heydorn, 1981). Whether or not interactions between currents and topography may lead to a stepping stone process (Hubbs, 1959) between seamounts (Etter & Mullineaux, 2001) requires further work to elucidate.

Despite the potential for barriers, distance, and limited dispersal abilities in some species to prevent genetic exchange between seamounts, there is relatively little conclusive evidence demonstrating that isolation leads to genetic dissimilarity between seamounts. The exception to this is two studies (Bucklin *et al.*, 1987; Samadi *et al.*, 2006) reporting genetic differentiation in seamount species due to limited dispersal potential. Genetic heterogeneity occurs among populations of an amphipod between the summit and base, but not the base and an adjacent abyssal site, reflecting the 'predominantly horizontal' dispersal of the species (Bucklin *et al.*, 1987). Mitochondrial DNA for a gastropod with direct developing larvae and limited dispersal ability displays genetic isolation along the Norfolk Seamounts (Samadi *et al.*, 2006). However, this study lacks context as it does not demonstrate that these divergence rates are higher than those expected for equally distanced populations in a connected system. The other five invertebrate species analysed from the Norfolk Seamount display no evidence of genetic isolation (Samadi *et al.*, 2006). An examination of bamboo corals also revealed a surprising amount of genetic similarity between distant populations (Smith *et al.*, 2004). Genetic differentiation exists in the blackbelly rosefish, *Helicolenus dactylopterus*, but only over

trans-ocean distances and not within individual regions. Similarly, the Antarctic butterfish, *Hyperoglyphe antarctica*, on seamounts off Australia, failed to yield any variation in enzymes for any locus (Bolch *et al.*, 1993). Over 1700 km, a common bivalve of California seamounts, *Acesta morei*, exhibits no genetic differentiation (Jones *et al.*, 2006). Some morphological analyses do indicate differences among seamounts (reviewed by Rogers, 1994), but in the light of molecular work these probably represent plastic responses to local environmental conditions, rather than genetic isolation.

Differences in dispersal capabilities in combination with isolation should also generate other island biogeographical phenomena on seamounts. Species with better (long-lived) dispersal phases are hypothesized to dominate seamount communities (Parker & Tunnicliffe, 1994). Alternatively, seamounts could possess more species with limited dispersal due to founder effects (Johannesson, 1988; Parker & Tunnicliffe, 1994). However, few studies address such issues, so the evidence is too sparse to refute either hypothesis (Leal & Bouchet, 1991; Parker & Tunnicliffe, 1994).

The perceived isolation of seamount faunas and resemblance to true islands has resulted in an examination of, and dialogue on, endemism. As some authors note (e.g. Rogers, 1994), the complicating factor for addressing endemism is the inability to characterize a seamount fauna and the regional, non-seamount pool successfully. At present, it is unlikely that we have identified enough of the regional or global deep-sea fauna to use the term endemic with any confidence. Only 200 seamounts of the potential 14,000 have been sampled (Stocks, 2004). Of the rest of the deep sea (>200 m, c. 306,036,300 km²), an extremely high estimate for the area sampled would be 0.5%, roughly the size of Alaska. The estimate of 0.5% also unrealistically assumes that the total fauna has been taxonomically described. For perspective, this would be equivalent to terrestrial biogeographers making claims of island endemism with only knowledge of the continental fauna from an area the size of the Netherlands.

Perhaps the first treatment of seamount endemism came from Wilson & Kaufmann's (1987) review, which divided seamount biota into biogeographical categories: endemic, provincial, exotics and cosmopolitan. The authors report rates between 0 and 36% for various seamount faunas. Notably, Wilson & Kaufmann (1987) preface the discussion with a comment that 'the endemic categories may be overestimated in many cases' due to many taxonomic groups being poorly studied. A resurgence of interest in seamount endemism was generated by the highly cited paper of De Forges *et al.* (2000). They report 29–35% of the 850 macro- and megafaunal species collected from seamounts in the Southwest Pacific were new to science and *potentially* seamount endemics. These estimates appear extraordinary until compared with those from 'typical' deep-sea mud floor. For slope communities off the eastern USA, Grassle & Maciolek (1992) note that 'Of all species, 58% (460) [of 798] are new to science'. Irrespective of the habitat, seamount or not, nearly any area of the deep sea will yield a substantial number of new species or *potential*

endemism, given the severity of undersampling this enormous system.

Other studies have not reproduced the high rates of *potential* endemism. Only between 5.6% and 6% of the polychaete fauna on seamounts in the eastern Atlantic are reported to be potential endemics (Gillet & Dauvin, 2000, 2003). Gastropods display equally low estimates of potential endemism in the Atlantic (Avila & Malaquias, 2003; Oliverio & Gofas, 2006). In an exhaustive effort to characterize Galatheid crabs on seamounts near New Caledonia, Samadi *et al.* (2006) found only a single species out of 70 not also present on the adjacent slope. Rowden and colleagues report 5.5% and 15% from the Kermadec volcanic arc and Chatham Rise, respectively (Rowden *et al.*, 2002, 2003).

If one assumes the reported percentages of endemism, c. 5–35%, do not reflect undersampling but rather actual values, they are still not particularly remarkable. For hydrothermal vents, endemism approaches 75%, with 60% of gastropods specifically tied to the habitat (Tunnicliffe *et al.*, 1998). For invertebrates on terrestrial islands, land snails approach 100% endemism on several islands around the globe, c. 800 Drosophilidae species are known only from the Hawaiian islands, and c. 50% of the insect fauna of the Canary Islands is endemic (Whittaker & Fernández-Palacios, 2007).

Are seamounts oases?

Recently, Samadi *et al.* (2006) formalized the 'oasis' hypothesis, positing that seamounts are 'places where a high trophic input allows abundance of species and high population densities...'. The hypothesis suggests two separate arguments: (1) seamounts are areas of high faunal biomass, and (2) this in turn supports greater species wealth. Historically, the desert oasis analogy has, in simplest form, referred only to an increase in biomass in comparison with the surrounding habitat (Carney, 1994). Although extensions of the analogy include more on isolation and diversity, this serves only to entangle several distinct hypotheses (e.g. seamounts are islands or biodiversity hotspots). I suggest that the oasis hypothesis should refer only to heightened biomass, and discussions about diversity should be framed in separate, more appropriate hypotheses.

The oasis hypothesis stems from two patterns encountered on some seamounts. First, seamounts often contain astounding densities of filter feeders, such as corals and sponges (Roberts & Hirshvield, 2004). Transects over Davidson Seamount indicate a drastic increase in invertebrate biomass over the summit not seen on the surrounding seafloor or adjacent margin (personal observation). Second, there is a well documented pattern of increased concentrations of commercially important fish species over seamounts (Rogers, 1994; Froese & Sampang, 2004; Genin, 2004). Estimates of biomass for other taxonomic groups, particularly the macro- and meiofauna, are sparse. However, meiofaunal organisms, such as forams, can occur in very low densities on seamounts compared with the surrounding area (Heinz *et al.*, 2004).

Some suggest that the dense fish aggregations over seamounts reflect enhanced primary productivity due to hydrographic effects resulting in increased macroplankton (reviewed by Genin, 2004). This idea of high trophic input is also proposed by Samadi *et al.* (2006). Increased chlorophyll *a* concentrations are documented over a few seamounts (Dower *et al.*, 1992; Dower & Mackas, 1996; Genin, 2004). Yet other seamounts in both the Pacific and Atlantic Oceans do not appear either to receive increased carbon flux (Verlaan, 1992) or to enhance zooplankton production (Fischer, 2005). Genin (2004) concludes that it is unlikely for upwelling and enhanced production to lead to animal aggregations, but rather they reflect a biophysical coupling between currents and animal behaviour.

Thus it is unlikely that seamounts receive increased trophic input. But the concept of high benthic biomass as it pertains to filter-feeding megafauna such as corals and sponges still begs for an explanation. However, if seamounts are oases, this is in contrast to insular systems which, due to reduced land area, typically have lower total resource availability, differentially affecting organisms with higher metabolic demands such as larger organisms and carnivores (Vermeij, 2004).

Are seamount coral gardens sponge meadows or hard substrates?

[Correction added after online publication November 2007: The above heading should read: Are seamounts coral gardens, sponge meadows, or hard substrates?]

Visually, the most prominent features of some seamounts are dense coral/sponge meadows and robust rock outcrops. Evidence does exist that these might be important, given the megafaunal community shift from one dominated by deposit-feeding on the background seafloor to filter-feeding on seamounts (Stocks, 2004), and the affinity of some deep-sea organisms for habitat provided by the coral (Roberts & Hirshfield, 2004). Biogenic structures may provide potential refuge from predation and control flow dynamics on the seafloor that alter community structure through recruitment (Jumars, 1975; Thistle, 1979a,b, 1983; Thistle & Eckman, 1988).

Neither of these habitats is confined to seamounts. Habitat-forming corals are found in dense aggregations in non-seamount localities (Etnoyer & Morgan, 2003, 2005) and hard substrate frequently occurs in canyons on continental slopes. Many of the filter feeders found on hard substrate on Davidson Seamount also exist on the walls of nearby slope canyons (J. Barry, personal communication). It is also important to note that many seamounts contain neither hard substrate nor coral/sponge meadows.

Are seamounts biodiversity hotspots?

Seamounts are hypothesized to harbour increased species richness (Samadi *et al.*, 2006). If seamounts are indeed biodiversity hotspots, then they are unlike islands, which

typically display diminished species diversity (Whittaker & Fernández-Palacios, 2007). To my knowledge, explicit and quantitative studies comparing benthic diversity, per unit of area, on and off seamounts in similar substrate, are rare. Foram assemblages appear to show little variation in diversity related to the seamount, but rather reflect differences in organic carbon content between stations. In general, top pelagic predators (e.g. birds, mammals, bony fish, cartilaginous fish, turtles) are found in higher diversity over seamounts, among other areas, related to the trapping of diurnally migrating plankton (Worm *et al.*, 2003).

Elevated richness might be predicted from the potential for increased biomass, increased speciation due to isolation, presence of habitat-forming corals and sponges, or habitat heterogeneity. As noted earlier, investigation of increased biomass of the majority of benthic groups is lacking, and evidence for high rates of endemism is tenuous. Some researchers suggest that deep-sea coral meadows in themselves possess extraordinary species richness. 'The number of species that live on these reefs has been estimated to be three times as high as on the softer surrounding seabed (UK Biodiversity Group, 2000)' (Husebo *et al.*, 2002). This statement is suspect, as little quantitative evidence supports this contention and comparison to soft substrate is superfluous. Still, if corals and other habitat types found on seamounts do have specific associated faunas, then seamount diversity might be elevated. Seamounts may also support high biodiversity through heightened beta diversity, reflecting turnover of faunas with depth and substrate type across the seamount.

Are seamounts just typical deep sea?

Soft sediments comprised of biogenic ooze and soft clay characterize a majority of the deep-sea floor (Gage & Tyler, 1991). Although recognized (Rogers, 1994), it is worth reiterating that not all seamounts contain hard substrate or lush coral/sponge groves, but rather look much like the surrounding deep sea floor. Regrettably, these communities seem to receive less attention than their more alluring cousins. It may be that a majority of seamounts are simply continuations of soft-sediment communities at comparable slope and rise depths. If this is the case, biodiversity of seamounts might indeed be higher than the surrounding seafloor, just as the slope and rise are generally more diverse than the abyssal plain (Rex, 1973; Rex *et al.*, 2005b). This increase in species richness at intermediate depths is posited to mirror (1) a shortened water column reducing the affect of remineralization; and (2) the increased organic input at those depths due to their proximity to productive coastal waters (Rex, 1981; Rex *et al.*, 1997, 2005a; McClain *et al.*, in press). The first might generate higher diversity in seamount soft-bottom communities than the surrounding seafloor. The second may mean that at comparable depths, and given current regimes, seamount soft-bottom communities may be less diverse than communities on continental margins.

CONCLUSIONS

To some extent, generalizations about seamounts are challenging, as seamounts should not be expected to function alike given varying bathymetry, substrate, currents and topography. For these reasons, habitats vary greatly over seamounts, including biogenically structured 'reefs', rock outcrops, fine-to-coarse sediments, and oxygen minimum zones. Nor should it be assumed that different parts of seamounts, for the same reasons, operate as a cohesive unit (Wishner *et al.*, 1990). For example, Davidson Seamount, off the central California coast, exhibits an intricate turnover in habitats from its base to summit (Lundsten *et al.*, 2006).

Many of the statements regarding seamounts as centres of endemism, islands, oases and biodiversity hotspots are either inappropriate or insufficiently examined to merit such a claim. Seamounts often do not experience isolation, as larvae are able to settle and sometimes connect even distant communities. Barriers to dispersal, such as Taylor columns, appear unlikely over most seamounts. The reported high proportion of endemic species reflects undersampling and never approaches those percentages found on true islands. Seamounts are unlikely to be oases, except perhaps for filter-feeding megafauna, but this is unlikely to reflect increased organic flux. Whereas seamounts might be biodiversity hotspots for top pelagic predators, there has been little investigation on whether the same holds for much of the benthic fauna.

In his excellent review, Rogers (1994) noted that most questions regarding seamounts are incompletely answered due to variety of geographical areas, aspects of biology studied, data quality, faunal group and sampling method encountered in the literature. Over 10 years later, this is still true. Although obvious, it is important to emphasize that more research in terms of both field sampling and the development of theory is needed to address many of these hypotheses more adequately. Recommendations for further research include the following:

1. If some seamount faunas do prove to function ecologically and evolutionarily as islands, then a variety of exciting and currently unexplored questions related to island biogeography exist. These range from hypotheses about island species–area relationships, species abundance distributions, assembly and nestedness of communities, ecological release, density compensation, niche shifts after bottlenecks, and gigantism/miniaturation of faunas (Whittaker & Fernández-Palacios, 2007).
2. The evidence for isolation in studies demonstrating community dissimilarity over large distances lacks context until shown to be greater than that of continuous systems (e.g. a specific isobath on continental margins or the abyssal plain). The same applies to genetic differentiation in direct developing species. More sophisticated techniques to evaluate spatial turnover, such as distance–decay analyses (Nekola & White, 1999), may provide more insight into these patterns.
3. More research is needed to explore seamount isolation at the species level utilizing molecular methods. Equally important is that negative results (no genetic dissimilarity among populations) are reported.

4. More caution is required in the use of the term 'endemic' in light of the extreme undersampling of deep-sea systems.
5. Interpreting the significance of endemism is hindered by the absence of studies quantifying the scale of seamount endemism. Examinations of seamount endemics should separate: (1) the number of species found only on seamounts, (2) the number of species found only on a particular seamount chain, (3) the number of species found only on individual seamounts, (4) the number of species restricted to a particular habitat on a seamount, and (5) the number of species found in a single sample, among replicate samples, on a single seamount or chain.
6. Comparison studies of diversity and standing stock on and off seamounts are essential to evaluating the hypotheses detailed here. Samples need to be quantitative (per unit area) and controlled for different substrate type and depth.
7. More attention should be given to separating and quantifying alpha, beta and gamma diversity with respect to seamounts.
8. Research is needed to examine the extent to which coral/sponge meadows are more probable on seamounts, given peculiar interactions of abiotic factors such as bottom topography and currents.
9. A careful examination separating the effects of hard substrate vs. coral/sponge aggregations on diversity, community structure and standing stock is essential.
10. Imperative for the development of any universal theory on seamounts is an expansion of predominantly megafaunal (e.g. corals and fish) focus, to include more work on patterns in macro- and meiofauna.

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BIOSKETCH

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