



BY TIMOTHY M. SHANK

Seamounts

Deep-Ocean Laboratories of Faunal Connectivity, Evolution, and Endemism



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ABSTRACT. Seamount systems that are geographically, hydrographically, topographically, and/or genetically “isolated” are likely to have developed highly endemic taxa and ecosystems. Although current estimates of endemism are challenged by inconsistencies in sampling approaches, the physical, biological, and geological processes intrinsic to seamount systems can undeniably serve to connect or isolate populations, stimulate genetic divergence, drive the formation of new species, and structure diversity and endemism. In fact, the large variety of interconnected mechanisms that promote or impede the genetic connectivity of seamount communities via dispersal (and the long-term maintenance of species or the subsequent divergence of populations leading to speciation) are key unknowns to understanding the fundamental evolutionary processes that structure both the diversity and biogeography of deep-sea fauna. Fortunately, the net results of these ecological interactions at seamounts are represented in the patterns of genetic connectivity of the constituent species. The conclusions of the relatively few genetic connectivity studies across seamount fish, coral, and invertebrates are largely inconsistent, reflecting the ecological and evolutionary complexities of seamount systems. Yet, identifying the “connectivity” of seamount populations and their diverse ecosystems, which are increasingly vulnerable to threats from destructive fisheries and mining practices, is vital for developing and evaluating conservation and management strategies for seamount resources. Integrated, multidisciplinary studies of the physical, chemical, geological, and ecological dynamics of seamounts will continue to reveal the value of seamounts as natural laboratories in which to gain insights into the factors that elucidate the role these systems play in the dispersal, evolution, and biodiversity of deep-sea fauna. These studies will also direct the management of seamount biological diversity, which is increasingly susceptible to anthropogenic disturbance.

INTRODUCTION

Seamounts are present throughout the world ocean across a wide range of latitudes and depths, and have diverse geological histories and ages (Kitchingman et al., 2007; Staudigel and Clague, 2010). Most seamounts are volcanic in origin and provide an elevated habitat with hard substrates and accelerated currents in realms largely dominated by relatively flat abyssal plains (Fryer and Fryer, 1987; Epp and Smoot,

1989; Batiza, 2001). Although the existence of seamounts has been known since the nineteenth century, our notions of how these deep-sea promontories host biological communities; what factors are important for creating, structuring, and maintaining biodiversity (Figure 1); and their role in structuring marine biodiversity and biogeography have largely developed over the last 20 years (reviewed by Clark et al., 2010a).

BIOLOGICAL “ISLANDS” IN THE DEEP SEA

One of the earliest views of seamounts was that they acted as stepping stones for fauna, facilitating communication among populations in the deep abyss (Hubbs, 1959), countering isolation and endemism. More recently, it has been hypothesized that the geographic distance between seamounts, and topographic and hydrographic conditions associated with seamounts, contribute to faunal isolation and the accumulation of highly endemic taxa (Rogers 1994; McClain, 2007). Comparisons of Southwest Pacific seamount and deep-sea hydrothermal vent endemism (Richer de Forges et al., 2000) strongly suggest that seamounts can be considered biologically distinct, isolated topographic features, or island ecosystems hosting abundant yet distinct faunal assemblages of octocorals, antipatharians, stylasterids, sponges, and more than 1300 other invertebrate species worldwide (Figure 1; see Box 7 on page 128 of this issue [Etnoyer, 2010]; Roberts et al., 2006). The Seamount Endemism Hypothesis (McClain, 2007) was first born when Wilson and Kaufmann (1987) found that 12–15% of all seamount species were endemic (endemic defined here as species inhabiting a single seamount or group of seamounts and absent elsewhere in the ocean). Subsequent estimates of seamount endemism exceeded 30–40%, and in one case up to 52% for benthic invertebrates (Parin et al., 1997; Richer

de Forges et al., 2000; Koslow et al., 2001). Adjacent seamounts in the New Caledonia area were found to share an average of 21% of their species, while less than ~ 4% of their species were shared on mid-ocean ridge seamounts separated by

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~ 1000 km (Richer de Forges et al., 2000).

Such estimates were intensely satisfying when physical oceanographic phenomena (i.e., rectified current flows) were thought to provide an inherent mechanism for how individual seamounts could be considered “isolated.” Isolation would occur by larval retention, thereby prohibiting larvae from leaving a seamount (Mullineaux 1994; see Lavelle and Mohn,

2010), isolating populations and species (Brewin et al. 2009), creating new species and increased endemism (McClain 2009), and ultimately regulating deep-ocean biogeography and evolution (Cho and Shank, in press). So, while seamounts could conceivably promote dispersal (Hubbs, 1959) via pathways of habitat stepping stones between continental edges and mid-ocean ridges, and across large stretches of deep-ocean basin



and boundary currents, the mounting evidence was that endemism due to “geographic or hydrographic isolation” was higher on seamounts than other marine habitats (Richer de Forges et al., 2000). The rates of new species discovery on seamounts were rapid, and yielded similarly rapid claims of high apparent endemism (see Box 10 on page 145 of this issue [Stocks, 2010]; Stocks et al., 2004; Stocks and Hart, 2007).

Subsequent studies indicated that the evolutionary role seamounts play in creating endemic islands is far more complicated. Follow-on surveys compared seamounts and adjacent slopes in the Austral-New Zealand region and revealed relatively few endemic species (e.g., Samadi et al., 2006; Hall-Spencer et al., 2007), with many species widely distributed within a specific depth range or having near-global distributions

(Smith et al., 2004a; Roberts et al., 2006; Samadi et al., 2006; McClain et al., 2009). Surveys of seamount-associated fish revealed much lower estimates (< 10%) of endemism (Fock et al., 2002; Stocks and Hart, 2007). These results ushered in new debates about sufficient faunal sampling on adjacent slopes and ridges (e.g., O’Hara, 2007), and a consistent comparative means of species identification (including genetic comparisons;

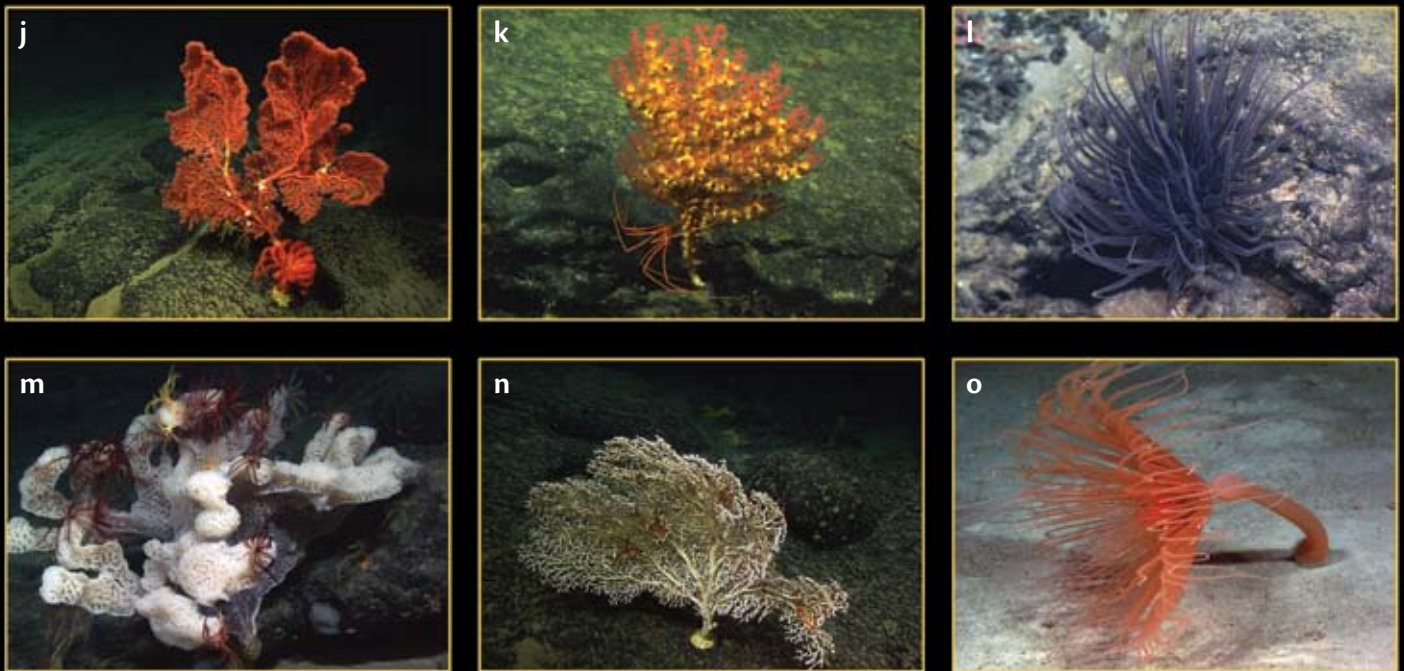


Figure 1. Faunal diversity in Northeast Atlantic seamount ecosystems, illustrating habitat-forming coral host and invertebrate associate relationships on the New England and Corner Rise seamounts (between 700- and 2100-m depth). (a) The scleractinian coral *Enallopsammia* sp. on Yakutat Seamount. (b) Sponge *Farrea* sp. on Yakutat Seamount. (c) Antipatharian coral *Plumapathes* sp. on Caloosahatchee Seamount (Milne-Edwards peak). (d) Ophiuroid *Asteroschema clavigera* on the octocoral *Paramuricea biscaya* on Yakutat Seamount. (e) *Anthomastus* coral sp. on Rehoboth Seamount. (f) Purple plexaurid coral on Yakutat seamount (g) Gerionid crab on the summit of Yakutat Seamount. (h) Coral *Iridogorgia magnispiralis* with barnacles *Glyptelasma* sp. at the tip on Nashville Seamount. (i) Shrimp *Bathypalaemonella serratipalma* among the branches of a *Chrysogorgia* sp. octocoral on Yakutat Seamount. (j) Coral *Paragorgia* sp. with a brisingiid seastar on the base on Manning Seamount. (k) Coral *Paragorgia* sp. covered with yellow zoanths and a pycnogonid spider on Balanus Seamount. (l) Actinarian anemone on Kelvin seamount. (m) Sponge with two species of crinoids (purple and yellow) on Kelvin Seamount. (n) Coral *Paragorgia* sp. with ophiuroid *Asteroschema clavigera* on Manning Seamount. (o) Ceriantharid tube anemone on Corner Seamount (Kukenthal peak). Frame-grabbed images acquired from high-definition video taken by the remotely operated vehicle Hercules imaging systems—an Insite Pacific Zeus HDTV camera (resolution 1035i) operated by the Institute For Exploration, University of Rhode Island (DASS Scientific Party)

Thoma et al., 2009), providing little confidence in any estimates of seamount endemism on a regional or global scale (Rogers et al., 2007). The most-cited problem that has made it difficult to distinguish true local seamount endemism is sampling biases, including differences in trawling gear, sampling effort on neighboring seafloor, limited taxonomic identifications, inability to successfully characterize seamount fauna coincident with the regional non-seamount pool, and the occasional collection of rare but widespread species (e.g., McClain, 2007; O'Hara, 2007). With fewer than 200 of the 14,000 seamounts (recognized minimum number) sampled even modestly, it is highly unlikely that seamounts have been sampled enough for any generalization on endemism. According to McClain et al. (2009), it is the equivalent of terrestrial biogeographers making claims of global endemism with only knowledge of the continental fauna in an area the size of the Netherlands. Indeed, given potential levels of cryptic (morphologically indistinguishable but genetically distinct) species in the deep sea (e.g., Vrijenhoek et al., 1994), estimates of endemism will only generate more uncertainty until significantly more effort is directed into sampling diverse seamount and regional deep-sea habitats, and using morphology and genetics for taxonomic identity (e.g., Thoma et al., 2009).

Irrespective of estimates of endemism, the physical, biological, and geological processes intrinsic to seamount systems can undeniably serve to link or isolate populations, stimulate genetic divergence, drive the formation of new species, and structure diversity and endemism. Seamount systems thus

present exceptional opportunities, if not “laboratories,” to examine these processes in the deep sea. The fact that seamount species are not shared among neighboring seamounts throughout known deep-sea biogeographic provinces (e.g., Watling, 2009) brings to the fore that seamounts at some temporal and spatial scales form isolated “islands” in the deep sea. Islands, by definition, are isolated in that a barrier obstructs the exchange of genetic information between two populations of a species (MacArthur and Wilson, 1967; McLain et al., 2009). This definition places a premium on understanding the processes that impact population connectivity.

IMPORTANCE OF POPULATION CONNECTIVITY

Population connectivity is defined here as the dispersal, survival, and reproduction of migrants so that they contribute to the local gene pool (Hedgecock et al., 2007). In essence, marine species are cohesively maintained in their geographic distribution by successful dispersal, colonization, and reproduction—and ultimately the exchange of their genetic material over time. The demographic connectivity of populations can not only regulate community composition through the dispersal of juveniles and motile adults, but also strongly affect biodiversity and the ability of ecosystems to recover from disturbance (Cowen and Sponaugle, 2009; see *Oceanography* issue 20-3 dedicated to marine population connectivity, available at http://tos.org/oceanography/issues/issue_archive/20_3.html). The demographic connectivity of populations relates to the ability of the species to respond to disturbance

or establish populations. Hence, how well we understand the connectivity of threatened and vulnerable species populations is fundamentally linked to how we design strategies to manage and conserve their populations.

The impact of intense or long-term fisheries activities on the structure and diversity of seamount communities is now at the forefront of concern for ecosystem and fisheries managers interested in developing marine protected areas focused on seamounts (see Spotlight 7 on page 146 of this issue [Clark et al., 2010b] and Spotlight 4 on page 104 of this issue [Shank, 2010]). Sessile seamount fauna and the ecosystems they support are, in the parlance of American policymakers and resource managers, “vulnerable marine ecosystems.” In particular, cold-water corals and sponges play host to a broad array of associated species (more than 1300; Roberts et al., 2006), including commercially important fish species, making them of immediate interest to conservationists, commercial fisheries managers, and scientists alike. In particular, the collateral damage from deep-sea trawling on the complex, long-lived, potentially highly endemic and poorly known benthic seamount communities has become central to high-seas conservation and fisheries management efforts. Well more than 76 fish species have been commercially harvested from seamounts (Rogers, 1994), and with many pelagic stocks still in decline, fisheries are searching deeper and deeper to maintain adequate catches (Stockley et al., 2005), leading to the observation of deep-water trawling damage in many areas around the globe (see Box 9 on page 132 of this issue [Clark, 2010]; Probert et al., 1997;

Koslow and Gowlett-Holmes, 1998; Freese et al., 1999; Bett, 2001; Brooke, 2002; Hall-Spencer et al., 2003). Recently, intense trawl damage, including denuded summits and massive piles of coral rubble on the Corner Seamounts, North Atlantic, was discovered (see Spotlight 4 on page 104 of this issue [Shank, 2010]; Waller et al., 2007) following seemingly modest international fisheries activities in the 1970s.

Specifically, understanding connectivity and the formative role seamounts play in the evolution and endemism of species, as well as in contemporary demographic processes (e.g., reproduction and colonization) that structure benthic seamount populations, are critical for managing the impacts of anthropogenic activities (e.g., fisheries and mining activities) and designing measures to identify and conserve vulnerable populations and ecosystems.

We now know that on seamounts there are intricate and complex interactions among hydrographic processes, seafloor features, and the intrinsic life histories of individual species that promote or impede the successful dispersal, colonization, maturation, reproduction, and genetic contribution to the next generation of fauna. Understanding the “connectivity” of marine populations is vital for conservation and fisheries management, yet the problem to be solved is understanding the movement of individuals and their contribution to the gene pool (Cowen et al., 2007).

CONNECTIVE PROCESSES

Broadly, the mechanisms that promote or impede the genetic connectivity of seamount communities via the dispersal

of larvae, juveniles, and motile adults, and thereby the long-term maintenance of species or the subsequent divergence of populations leading to speciation, are key unknowns to understanding the fundamental evolutionary processes that structure both the diversity and biogeography of deep-sea fauna.

Connectivity among populations can be affected by a wide range of factors, the most obvious of which are physical

relative to hydrographic conditions and geographic distance between seamounts and other suitable habitat; and (6) the differential rates of larval settlement, colonization, maturity, and mortality. These numerous factors are intrinsically and complexly interconnected (Figure 2), and all variously impacted by natural and anthropogenic disturbances. The ability to assess and resolve their relative importance at

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barriers to dispersal that restrict the exchange of migrants or colonizers among populations (Pineda et al., 2007). At seamounts, these factors include: (1) differences in depth-induced restriction or zonation of marine species; (2) hydrographic conditions—including the tendency of impinging circulation to retain particles/larvae and expose suitable hard-bottom habitats that in turn support emergent filter-feeding epifauna such as corals, crinoids, and sponges; (3) differences in reproductive life-history strategies; (4) temporal food subsidies provided by layers of plankton moving by stationary seamounts; (5) species-specific dispersal capabilities

any particular point in time is made only more difficult, in that they are transient in their interactive strength among species and occur over different temporal and spatial scales.

For example, the interactions between oceanographic currents and seamounts range in scale from the deflection of major oceanographic currents, to the promotion of local upwelling and enhancement of nutrient delivery, to the trapping of vertical migrators, and dominance of local detritus-based food webs, to the scouring of seafloor sediments yielding substrate favorable to recruitment by sessile organisms (Rogers, 1994; Pitcher and Bulman,

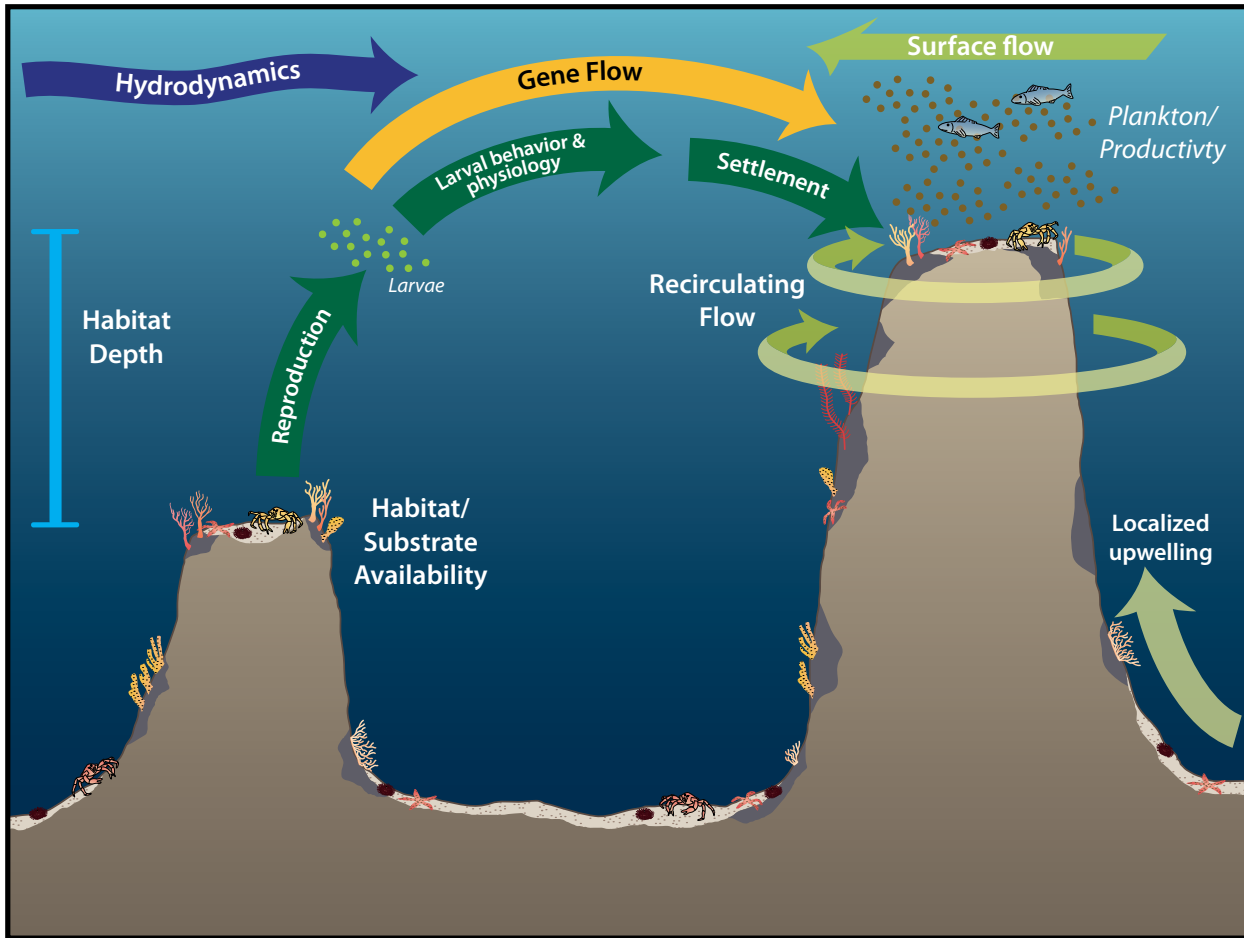


Figure 2. The complex interaction of extrinsic (e.g., physical hydrodynamics) and intrinsic (e.g., species-specific larval physiology) factors that influence the dispersal, colonization, and genetic connectivity to either maintain species cohesion or foster population divergence leading to speciation. The effective conservation and management of vulnerable seamount ecosystems is linked to the understanding the genetic connectivity of species populations.

2007). Transient recirculating retention cells can be generated by steady ambient current flow around a seamount if the surrounding water is unstratified or by tidal rectification (i.e., residual mean currents of tidal flow) above a seamount. Examples have been observed at Cobb and Fieberling seamounts in the Pacific, and Great Meteor Seamount in the Atlantic (reviewed by White et al., 2007). Consequential impacts on larval dispersal include the retention of planktonic larvae via the trapping of

impinging oscillations to the seamount topography, depending on seamount diameter, relative water-column height, and slope of the seamount's flanks (Beckmann, 1995). Importantly, such circulation could restrict certain fauna from using seamounts as stepping stones, potentially shifting population dynamics toward isolation, growing genetic divergence, and ultimately the creation of new species (as defined by both reproductive isolation and phylogenetic definitions, *sensu* Cracraft, 1983).

Although it is currently impossible to ascribe directly, and with any certainty, any single factor or interaction of factors controlling the connectivity of individual seamount species, population genetic approaches can provide an immediate assessment as to their historical or contemporary interaction. Regardless of any assigned cause or correlation among the factors, populations evolve by changes in the frequencies of alleles, the alternative forms of genes that constitute heritable diversity among conspecific

individuals. Allelic-frequency change results from evolutionary forces: *mutation* of genes; *random genetic drift* caused by stochastic fluctuations in the demography of finite populations; *gene flow*, resulting from migration among populations; and *selection* within and among populations. Random genetic drift and diversifying selection can cause populations to diverge, for example, while migration acts to homogenize populations and to maintain the genetic cohesion of a biological species. The genetic composition of seamount populations thus represents the net result of the physical, chemical, and biological processes depicted in Figure 2 and is an important approach for rapidly assessing these interactions.

The use of DNA sequences, DNA microsatellites, and other genetic markers has provided a comparative phylogenetic and population genetic framework to test predictions of genetic isolation and structure derived from the various factors described above, and has contributed to the merging of population genetic and phylogenetic studies (Slatkin and Barton, 1989; Edwards 1993). Genetic variation fluctuates within and among these genetic markers, so that the choice of marker used depends directly on the temporal and spatial scale of the question being asked, particularly for groups of closely related species (Avice et al., 1987). Detailed information on genetic markers and approaches can be found in *Oceanography* issue 20-3 dedicated to marine population connectivity (see http://tos.org/oceanography/issues/issue_archive/20_3.html). In general, marine population genetic studies examine the variation and distribution of gene or DNA sequences' frequencies

to locate divergence and structure and attempt to relate or correlate these resulting genetic measures and patterns of connectivity to extrinsic physical factors properties (e.g., inferred mode of dispersal). These same approaches have been used in the few studies of seamount population genetic connectivity.

GENETIC CONNECTIVITY AND SEAMOUNTS

Almost all genetic studies of seamount fauna to date have been conducted with the ultimate objective of understanding whether or not seamounts and their associated physical oceanographic properties, habitat availability, and other features facilitate the genetic isolation of populations and species, and thus ultimately influence the biogeography and evolution of deep-sea fauna. Most of these studies have included seamount-related fauna to determine taxonomic identity and evolutionary relationships of species. They have almost exclusively been focused on cold-water corals. For example, France and Kocher (1996), Song and Won (1997), and Bernston et al. (1999, 2001) examined the deeper evolutionary (and systematic) relationships among the Anthozoa, in many cases combining molecular and morphological systematics to resolve taxonomic classifications. Similar genetic studies in scleractinian corals (La Goff-Vitry et al., 2004) and octocorals (Berntson et al., 2001; Sánchez et al., 2003) have also been undertaken. These studies that define species boundaries and determine species designations are a critical prerequisite for the identification of intraspecific populations for the pursuit of population genetic studies on seamounts.

Although the importance of

understanding genetic connectivity of seamount fauna is accepted as vital to understanding processes underlying taxonomic and evolutionary processes, only a handful of published studies have had their primary focus on seamount-to-seamount population connectivity.

Seamount-Associated Fish

Genetic studies involving commercially important fish revealed genetic homogeneity among seamounts at intraregional, regional, and oceanic geographic scales, including at the slopes of continental margins, and oceanic islands (e.g. Martin et al., 1992; Sedberry et al., 1996; Hoarau and Borsa, 2000). Species such as the northern Pacific pelagic armourhead (*Pseudopentaceros wheeleri*), the alfonsino (*Beryx splendens*), black oreo (*Allocyttus niger*), and smooth oreo (*Pseudocyttus maculatus*) did not harbor genetically distinct or geographically structured populations between seamounts, and continental and oceanic island slopes (Martin et al., 1992; Hoarau and Borsa, 2000; Smith et al., 2002). Similarly, across the North Atlantic, DNA microsatellite frequencies revealed homogeneous populations of wreckfish (*Polyprion americanus*) (Ball et al., 2000). The mitochondrial DNA marker 12S rDNA did not reveal genetic structure (Rogers et al., 2006) in the patagonian toothfish (*Dissostichus eleginoides*), but differences in microsatellite frequencies were detected between seamount and non-seamount populations, demonstrating the importance and utility of genetic markers depending on the temporal and spatial scale of the connectivity investigated.

In marked contrast, genetic differentiation has been identified among

populations of fish species located on seamounts, the continental margin of Europe, and the Azores Islands on the Mid-Atlantic Ridge (e.g., Stockley et al., 2005). Marked genetic differentiation of mitochondrial sequences between seamount and non-seamount populations of the Blackbelly rosefish (*Helicolenus dactylopterus*) corresponded to differences in depth (e.g., Aboim et al., 2005). In the southern Pacific, genetic differentiation was reported among populations of orange roughy (*Hoplostethus atlanticus*) (Smolenski et al. 1993; Smith et al. 1997) with genetically distinct populations (Smolenski et al., 1993). Mitochondrial DNA and microsatellite analyses of black sea bream (*Pagellus bogaraveo*) populations between slopes of the Azores Islands in the North Atlantic revealed significant (but low to moderate) genetic differentiation with evidence for a recent bottleneck, perhaps due to the impacts

targeted questions of connectivity should direct species-specific investigations for management.

Seamount Corals

Few population genetic studies of corals have been conducted on seamounts. This has largely been due to both the difficulty in obtaining statistically appropriate numbers of individuals to constitute a population viable for analyses, and the lack of genetic markers that provide intraspecific variation. Analyses of mitochondrial genes from corals of the genus *Keratoisidae* from across the Pacific Ocean revealed widespread distribution of haplotypes across large oceanic distances (Smith et al., 2004a), suggesting long-range dispersal and widespread gene flow. However, interpretation of these results is challenging, as evidence suggests that mitochondrial genes evolve slowly in octocorals (France and Hoover, 2002). These markers also

as a population marker of choice, but their development can be time and cost consuming. DNA microsatellite analysis of precious corals, continuous populations of red (*Corallium lauuense*) and pink (*Corallium secundum*), on the main and Northwest Hawaiian seamount chain, revealed population structure, small but significant genetic differentiation between populations within coral beds, between beds on the slopes of shared seamounts, between islands, and between islands and seamounts (Baco and Shank, 2005). Evidence of genetic isolation by distance (in *C. secundum*) and heterozygote deficiency suggested largely self-recruiting populations, with occasional long-distance dispersal. Similar investigations employing multilocus genetic markers in seamount corals are currently underway in both the Atlantic and Pacific.

Seamount Invertebrates

Early genetic studies of seamount fauna included the deep-sea amphipod *Eurythenes gryllus*, showing that individuals from the summit of Horizon Guyot were genetically distinct from individuals near the base of the guyot and at other deep-sea sites (Bucklin et al., 1987). Genetic homogeneity of *Eurythenes gryllus* populations was subsequently found within the same depth zone at the scale of ocean basins, but these populations were genetically distinct from those at different depths, indicating that depth may be an important factor influencing population structure of seamount invertebrates (France and Kocher, 1996).

More recently, Samadi et al. (2006) used haplotype frequencies of a mitochondrial gene (cytochrome oxidase I) in

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of fishing. In summary, the population connectivity among commercially important seamount and slope fish populations provides a varied and mixed portrait of genetic exchange, whereby

lack sufficient variability in primnoid corals to resolve morphological species (Baco-Taylor et al., 2008). Multilocus markers, such as DNA microsatellites, on the other hand, hold great promise

four species of squat lobster (three from the Family Galatheididae and one from the Family Chirostylidae) and two species of gastropods that were inferred to have different modes of larval development. From populations on the nine seamounts (and slope areas) off of New Caledonia, Southwest Pacific, genetic homogeneity was observed in all taxa over all locations with the exception of one species, the gastropod *Nassaria problematica*. Morphological evidence suggests this species hosts a nonplanktotrophic mode of development (often equated to lower dispersal distance) compared to the other four that show planktotrophic development. This study revealed not only a strong correlation of life-history strategy to realized connectivity, but demonstrates the power of examining connectivity factors (Figure 2) via testing for patterns of connective congruence across multiple species over the same geographic distribution.

Similar mitochondrial (COII) haplotype frequency analysis revealed significant genetic differentiation between populations of the commercially exploited lobster *Jasus tristani* located on Vema Seamount (and surrounding slopes) in the South Atlantic (von der Heyden et al., 2007). Small but significant genetic partitioning existed over a distance of 2000 km between Vema Seamount populations and all other locations. No population differentiation was detected among any of the non-seamount populations. Interestingly, the Vema Seamount population is viewed as failing to recover from fishing impacts, which is further confirmed by the genetic data that suggests the seamount population is largely self-recruiting (von der Heyden et al., 2007).

Seamount genetic connectivity studies have also included the investigation of hydrothermal vent species, as many seamounts occur on or proximal to mid-ocean ridges (e.g., Wantanabe et al., 2005). In particular, bathymodiolin mussel species on Kermadec Arc seamounts near New Zealand revealed heterogeneity in allozyme frequencies between seamounts and significantly high levels of genetic differentiation (with a notable lack of mitochondrial haplotype differences between two populations), despite the fact that these seamounts were separated by only 50 km (Smith et al., 2004b). Shallow depths, markedly different faunal composition (> 90%) between the two seamounts, and theoretical hydrodynamics that could retain larvae were invoked to explain the lack of dispersal through a hydrographic barrier.

Connectivity and Host-Associate Relationships

Recent observations of seamount coral ecosystems have revealed many associations between coral hosts and epibiotic invertebrates (Figure 3; Mortensen, 2001; Buhl-Mortensen and Mortensen, 2005). For example, along the New England and Corner Rise seamounts, *Metallogorgia affn. melanotrichos* Wright and Studer 1889 colonies appear to grow and develop simultaneously with a single (rarely, two) individual ophiuroid (brittle stars) of a single species (*Ophiocreas affn. oedipus* Lyman 1878) positioned at the center node of the branches (Mosher and Walting, 2009). *Candidella imbricata* Johnson 1862, a primnoid fan, is host to both potentially facultative ophiuroids (*Ophioplinthaca affn. abyssalis*) and an obligate polynoid polychaete

(*Gorgoniapolynoe caeciliae* Fauvel 1913; Eckelbarger et al., 2005). Over this same region, a *Parantipathes sp.*, a bottlebrush-shaped black coral, is host to a single species chirostylid galatheid crab—and 80% of the observations reveal a pair—one female and one male (unpublished data of author Shank).

Recently, Cho and Shank (in press) revealed patterns of dispersal and genetic connectivity of four species of ophiuroid (*Asteroschema clavigerum*, *Ophiocreas oedipus*, *Ophioplinthaca abyssalis*, and *Ophioplinthaca chelys*) inhabiting North Atlantic seamounts (including heavily fished areas). Analyses of mitochondrial 16S and COI genes revealed evidence for recent population expansion, and estimates of high gene flow for all four species throughout the region. However, when the data were specifically binned and analyzed by depth within seamount chains, significant genetic differentiation among populations was detected. No congruent pattern of historical migration was found between species and seamounts, which was in part attributed to narrow species-specific habitat requirements or varying levels of coral host specificity. The ecological and evolutionary significance of host-specific relationships on potentially isolated seamounts presents new fundamental questions. Are the epibionts (organisms that live on the surface of other living organisms) associated with one coral host genetically distinct from those same species found associated with other hosts? Are coral and associated faunal populations evolving in isolation if their coral host's larvae are retained in seamount-generated flows for long time periods? Given these intimate associations between specific coral

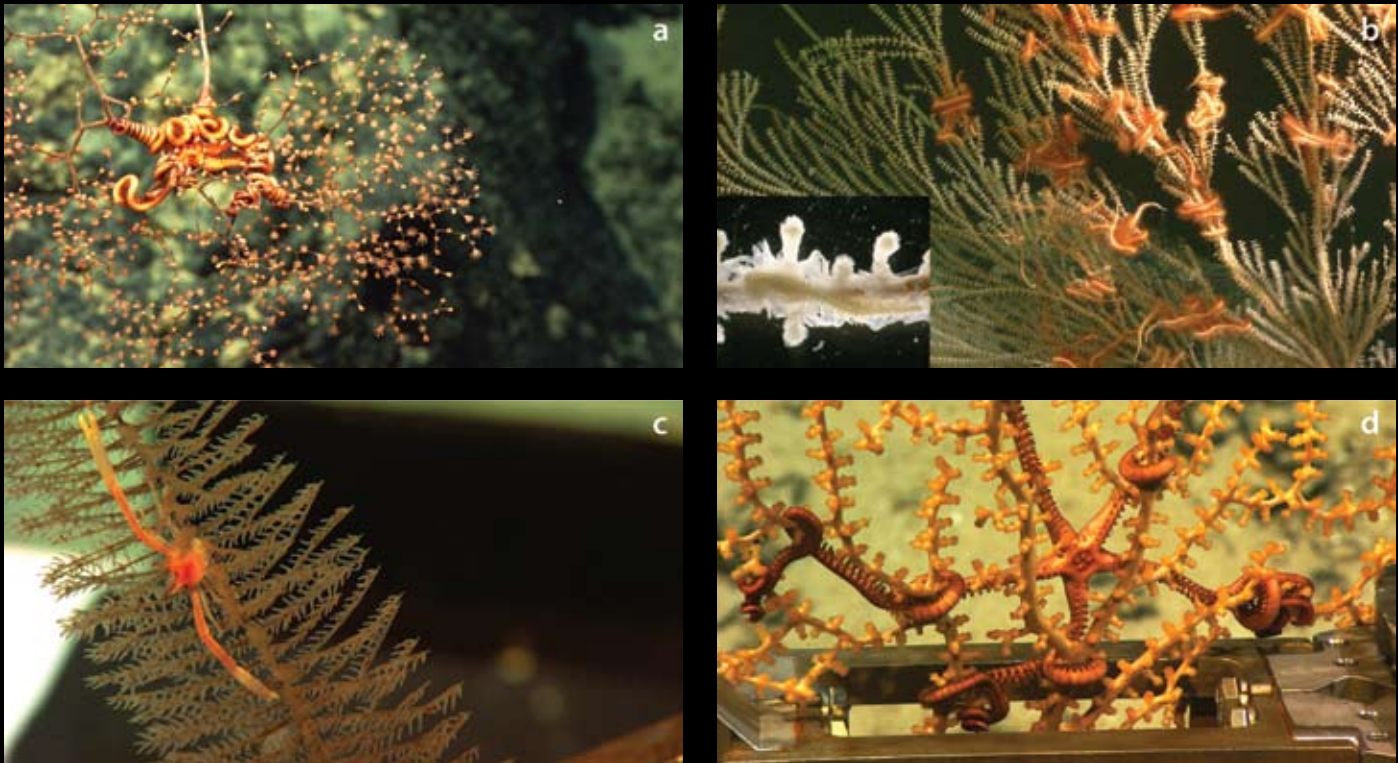


Figure 3. Examples of seamount invertebrate species and their specific habitat use of cold-water corals as hosts on the New England and Corner Rise seamounts (depth ~ 700–2100 m). (a) The octocoral *Metallogorgia melanotrichos* hosts only a single individual ophiuroid (brittle star) of the species (*Ophiocreas oedipus*; Mosher and Watling 2009) at the branching center of the coral. (b) The primnoid coral *Candidella imbricata* Johnson 1862 hosts numerous ophiuroids of the species *Ophioplinthaca abyssalis* and inset, the obligate polynoid polychaete (*Gorgoniapolynoe caeciliae*; Eckelbarger et al., 2005), live within tubes constructed by the host coral in response to the presence of this worm. (c) The bottlebrush black coral, *Parantipathes* sp., hosts a single species, and frequently a mature male and female chirostyliid crab. (d) Single individuals of a specific ophiuroid species, *Asteroschema clavigera*, inhabits *Paramuricea* octocoral species. The connective processes controlling the demographics of these and other host species may largely control genetic connectivity of these diverse coral associates. *Images credit: DASS 2005 Expedition, NOAA Office of Ocean Exploration and Research, and the Institute for Exploration*

and epifaunal species, an additional factor affecting the potential connectivity of seamount populations and the creation of endemic seamount fauna (adding to Figure 2) is the co-evolution or co-dispersal potential of closely interacting species that form host-associate relationships (Buhl-Mortensen and Mortensen, 2005; Mosher and Watling, 2009).

The results of seamount population genetic studies to date suggest that: (1) species-specific modes of dispersal (larvae, juveniles, and adults) can be correlated to patterns of genetic connectivity and structure; (2) dispersal, connectivity, or gene flow results of one species cannot be extrapolated to other seamount species, even closely related species sampled from the same

range (e.g., Aboim et al., 2005; Cho and Shank, in press); and (3) species with inferred “limited larval dispersal” can travel large oceanic distances. In short, genetic results on the connectivity of populations should be interpreted with caution. Given the rate of genetic change of different genetic markers, different molecular markers can yield markedly different results within the

same populations. Results need to be interpreted on the temporal and spatial scale appropriate to the rate of change and resolution of the marker for the target taxa and the connectivity question being asked. In the deep sea, and on seamounts in particular, sufficient population sampling of statistically appropriate numbers of individuals for the genetic marker should be considered (e.g., Thoma et al., 2009).

With the above results and the variety of complex formative factors impacting both endemism and connectivity of seamount species and populations, making generalizations about the connectivity and endemism among seamount taxa is challenging. Yet, when informed by physical, geological, and ecological information, such results can be highly useful for guiding the development of appropriate precautionary management approaches to conserve deep-water communities potentially impacted by the exploitation of biotic and abiotic resources.

Connectivity and Anthropogenic Disturbance

Deep-sea fisheries activities provide vivid examples of habitat destruction for species that require hundreds of years to reach maturity. Trawlers literally drag large nets equipped with steel rollers weighing thousands of pounds over seamount summits, scooping up everything in their 100-meter-wide paths (see Clark, 2010). We currently have limited knowledge of the dispersal of deep-water seamount fauna, including corals and their epifaunal associates; managers concerned with the protection of oceanic biodiversity need better information about the connectivity of

seamount populations. Specifically, with regard to the mining of old seamount crust (currently, there is a high interest in cobalt ores), there is an absence of fundamental and critical biological data (e.g., species present and connectivity estimates) on every candidate seamount in the southern equatorial Pacific. Without these data, as well as the careful consideration of issues related to the assessment of biological impacts of mining activities, ecologically targeted regulatory management of seamount ecosystems associated with mining operations will be difficult. These issues include: (1) the necessity that any plan assessing biodiversity, endemism, and connectivity include the integrated use of genetic approaches; (2) that one cannot reasonably extrapolate dispersal/connectivity results of any taxa from one seamount to another; and (3) that a seamount should not be considered isolated simply based on geographic distance or inferred hydrographic circulation patterns.

An “isolated” seamount should be considered “isolated” with regard to populations of a given species if the recent exchange of genetic information is not significant. By this definition, geographic distance is not equivalent to isolation.

Mining activities, including mapping, imaging, sampling, testing of ore-recovery systems, and the characterization of environmental impacts, can have potentially positive impacts on seamount biological science, including the discovery of new species, adaptations, ecologies, evolutionary pathways, and habitat information with which to develop and constrain models of connectivity and evolution of seamount

fauna. The commercial recovery of ores on seamounts also imparts collateral negative impacts, including habitat loss, prohibiting connectivity and reducing genetic diversity; degradation of habitat quality; local, regional, or global extinction of endemic or rare taxa; and decreased diversity (at all levels: genetic, species, phylogenetic, habitat) and loss of potential biological resources. Part of the arsenal of successful management of seamount ecosystems will be the development of long-range seafloor survey techniques (e.g., employing autonomous underwater vehicles) in concert with models predicting the location and abundance of vulnerable seamount ecosystems using integrative approaches. These approaches will include the knowledge of species reproductive strategies, regional and local physical oceanographic settings, and patterns of genetic connectivity to estimate the connectivity of seamounts and likely causative processes structuring species diversity.

FUTURE OUTLOOK

Genetic connectivity studies of vulnerable marine ecosystems on seamounts will increase for the purposes of both understanding how biodiversity is maintained in our ocean, and informing conservationists and managers. We need more data to rapidly assess whether or not populations of a species are evolving in isolation from other populations, whether seamount populations have a distinct history, perhaps congruent with the history of seamount formation or climate-induced shifts in circulation, whether or not disturbed habitat areas on a given seamount can be repopulated by larval and genetic exchange or one-way genetic communication

through dispersal and gene flow, and whether the populations of associated invertebrate species are co-evolving with slow-growing host species. Coordinated and integrated ecological studies of those processes that create and maintain the connectivity of species populations, including the experimental characterization of physical oceanographic circulation, reproductive and dispersal strategies, and recruitment and colonization dynamics of seamounts and their fauna will be integral to the future of assessing: (1) endemism—the taxonomic and systematic relationships of fauna among seamounts and deep-sea slopes, margins, and abyssal plains; (2) patterns of biogeography and endemism based on these taxonomic determinations; (3) the role seamounts play in shaping the dispersal, evolution, and biodiversity of deep-sea fauna; and (4) the balanced management of seamount resources, including metal-rich crust, hydrothermal deposits, and biodiversity that is increasingly susceptible to anthropogenic impacts. The significance of integrating genetic connectivity assessments with seamount resources is far more than a direct contribution to the scientific understanding of the connectivity of marine populations among seamounts. The provision of such dispersal information is also important for the proper management of fishery stocks, the design and implementation of marine reserves, and to international policymakers who will ultimately determine the fate of seamount mineralogical and biological resources.


CONCLUSIONS

Seamount systems foster a diverse range of habitats for deep-sea life, often focusing a productive supply of

nutrients, supported by a broad range of oceanographic and geological boundary conditions. These processes that genetically connect populations of species are governed by geological, oceanographic, and biological interactions that can create and maintain “biological hotspots” in the ocean, and ultimately control regional biodiversity, biogeography, and the evolution of deep-sea fauna. These same processes, however, may also serve to limit productivity, endemism, and the diversification of populations among individual seamounts and chains of seamounts. With additional multidisciplinary studies of the physical, chemical, geological, and ecological dynamics on seamounts, rapidly evolving theories and hypotheses will advance our ability to explain these observations in different ocean regions, from the influences of hydrographic boundaries, to depth and species-specific life history differences, to co-evolution and climate change. As such, seamounts will continue to provide natural laboratories in which to test and gain insights into the factors that elucidate the dynamic and variable role these systems play in structuring the evolution, connectivity, and diversity of deep-sea fauna.

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