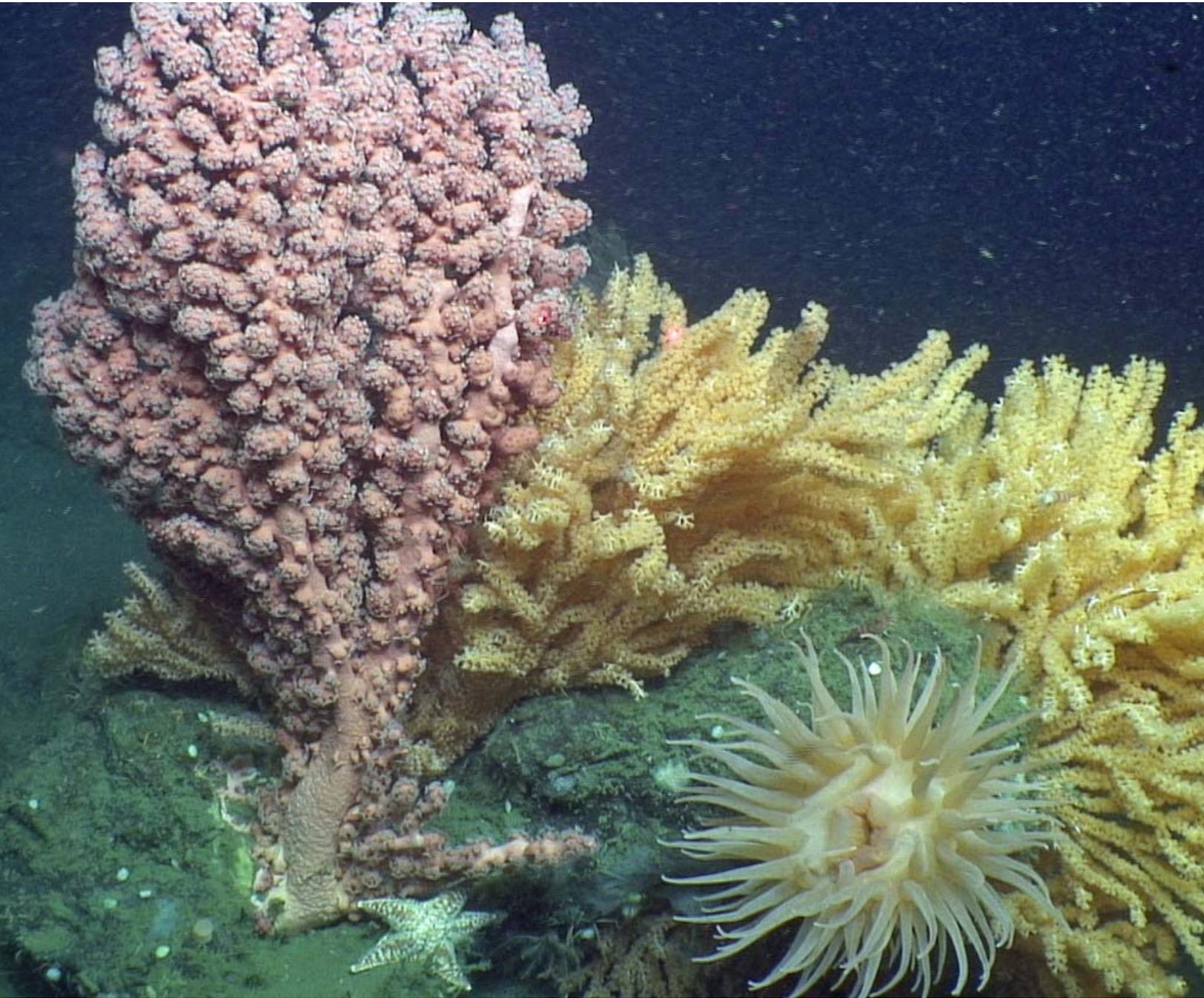


Population Connectivity of Deep-Sea Corals

Chapter 12 in The State of Deep-Sea Coral and
Sponge Ecosystems of the United States Report

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Red bubblegum coral (*Paragorgia* sp.) and several colonies of *Primnoa* sp. occupy a boulder in close proximity to an anemone and sea star in Norfolk Canyon. These taxa have been the subjects of population genetic studies. Courtesy of NOAA/BOEM/USGS.



POPULATION CONNECTIVITY OF DEEP-SEA CORALS

I. Introduction

Identifying the scale of dispersal among habitats has been a challenge in marine ecology for decades (Grantham et al. 2003, Kinlan and Gaines 2003, Hixon 2011). Unlike terrestrial habitats in which barriers to dispersal may be obvious (e.g. mountain ranges, rivers), few absolute barriers to dispersal are recognizable in the sea. Additionally, most marine species have complex life cycles in which juveniles are more mobile than adults. As such, the dynamics of populations may involve processes in distant habitats that are coupled by a transport mechanism. Studies of population connectivity try to quantify the transport, or dispersal of individuals, among geographically separated populations. For benthic marine species, such as corals and demersal fishes, colonization of new populations occurs primarily by dispersal of larvae (Figure 1; Shank 2010). Successful dispersal and recruitment, followed by maturation and reproduction of these new migrants ensures individuals contribute to the gene pool (Hedgecock 2007). Thus, successful dispersal links and cohesively maintains spatially separated sub-populations. At shorter time scales (tens to hundreds of years), connectivity regulates community structure by influencing the genetic composition, diversity and demographic stability of the population, whereas at longer time scales (thousands of years), geographic distributions are affected (McClain and Hardy 2010). Alternatively, populations may become extinct or speciation may occur if connectivity ceases (Cowen et al. 2007). Therefore, the genetic exchange of individuals between populations is fundamental to the short-term resilience and long-term maintenance of the species. However, for the vast majority

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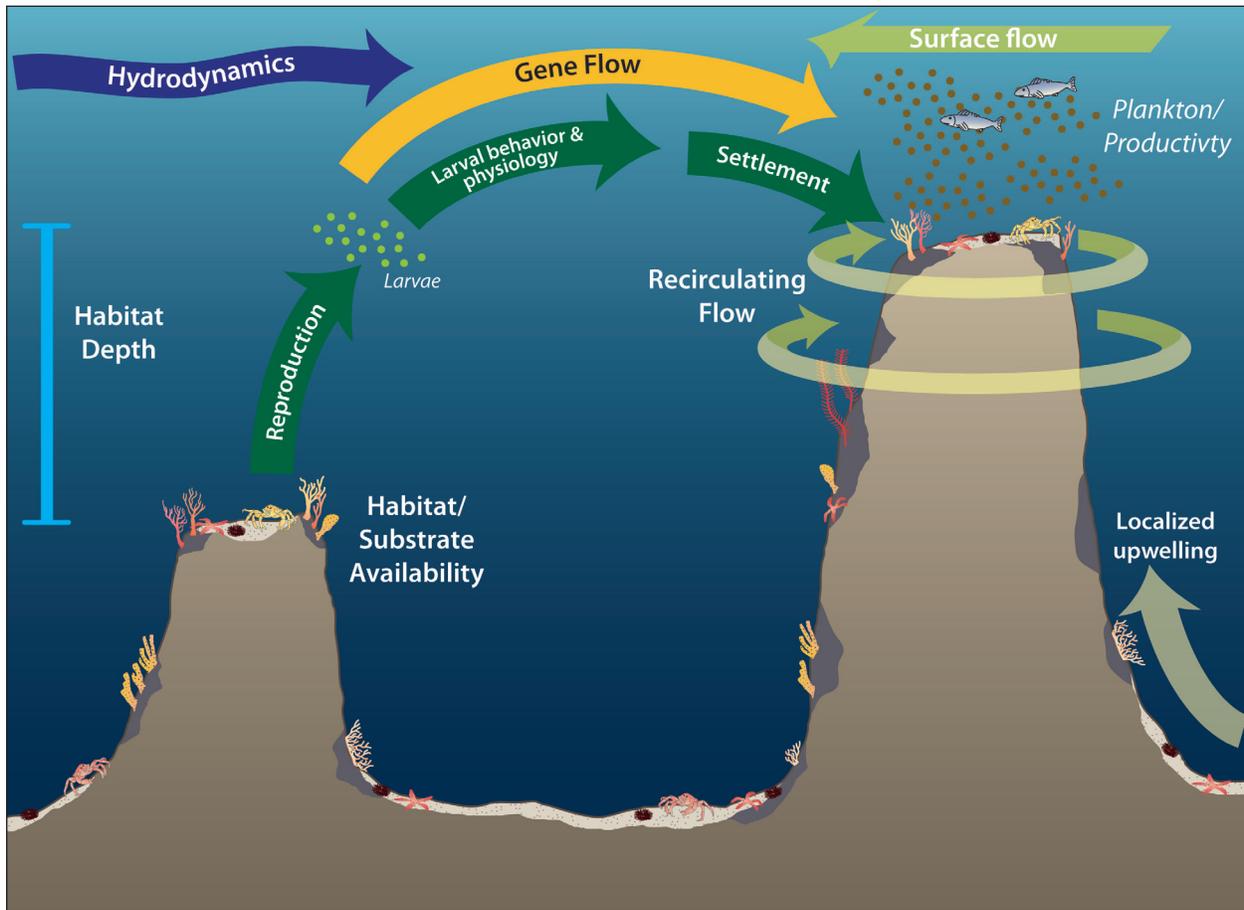


Figure 1. Diagrammatic representation of potential physical (hydrodynamics, depth) and biological (reproduction, larval behavior, settlement) forces that may influence dispersal, colonization, and genetic connectivity among deep-sea coral populations. (reprinted from Shank 2010, Oceanography; 1).

of marine species, population connectivity remains poorly understood.

To effectively manage marine species, knowledge of the spatial scale at which populations are connected is beneficial (Palumbi 2003, Fogarty and Botsford 2007). Ecosystems within the deep sea often occur over large geographic scales, yet are spatially fragmented across the entire range with stretches of unsuitable habitat separating prime habitat patches (e.g. cold-water coral reefs, methane seeps, hydrothermal vents). Habitat fragmentation may escalate with increasing resource exploitation (e.g. Hilário et al. 2015). The ecological patterns observed in

many deep-sea ecosystems can be explained by metapopulation dynamics as conceived by Levins (1969). Under this scenario, species occur within patchy habitats that undergo local extinction and recolonization and those patches are connected via dispersal and migration. The persistence, or viability, of the metapopulation increases as the availability of suitable habitat patches increases, local extinction decreases, and migration/dispersal between patches increases. In local deep-sea communities, the regional distributions of each species may be composed of metapopulations that are influenced by a balance among global-scale, landscape-scale and small scale dynamics (Levins et al. 2001).

Spatial management tools, such as networks of marine protected areas or reserves have the potential to protect the entire ecosystem, including nursery grounds, adult habitats, food sources, etc. Success of these protective measures relies at least partially upon estimates of dispersal rates across reserve boundaries (Botsford et al. 2003, Hilborn et al. 2004). For example, a population may be more vulnerable to human activities if it is not likely to receive recruits from other populations (e.g., self-sustaining populations, where only larvae produced within the population settle in the population). Alternatively, if larvae produced within a given population disperse to other populations, that population may be an important larval “source” that could rescue depleted populations (Pulliam 1988). Identifying source sub-populations is vitally important to management and conservation plans. Estimates of connectivity provide the relative scale at which a protected area may function. Such information may be utilized to optimize the placement of protected areas and to estimate the potential impacts to recruitment outside protected area boundaries (Palumbi 2001, Gaines et al. 2010).

Biological and physical processes influence larval dispersal (Cowen et al. 2007, Paternello et al. 2007, Galarza et al. 2009, Cowen and Sponaugle 2009, Sivasundar and Palumbi 2010, Mokhtar-Jamaï et al. 2011, Woodson et al. 2012). While biological attributes, such as timing of reproduction, larval behavior (e.g., swimming, vertical migrations), buoyancy, and physiology (e.g., feeding), affect larval survivorship and dispersal distances, physical processes, such as prevailing currents, eddies, recirculating flows, bottom topography and upwelling, can enhance or constrain larval movement (Figure 1; Shank 2010). Factors such as distance from a spawning site, advection and diffusion, and high mortality rates, all

influence the number of larvae present in the water column (Cowen and Sponaugle 2009, Rosser 2015). The combined influences of these biological and physical parameters may either promote dispersal of larvae over great distances (i.e. create dispersal corridors), or constrain population connectivity by isolating some populations from others (i.e. create barriers to dispersal).

Due to small larval sizes and the immense volume of the oceans into which larvae disperse, measurements of dispersal distances are difficult and tracking of spawning events can be quite challenging (Gawarkiewicz et al. 2007). Life history traits, such as pelagic larval duration, have been used as a proxy for dispersal distances. Pelagic larval duration correlated well with estimates of dispersal for some species (Bohonak 1999, Shanks et al. 2003). However, there are numerous examples where no relationship between pelagic larval duration and dispersal distance was observed (e.g. Severance and Karl 2006, Miller and Ayre 2008, Weersing and Toonen 2009, Galarza et al. 2009). Although the validity of correlation between pelagic larval duration and dispersal potential remains equivocal, it may at least set an upper bound on dispersal distance (Selkoe and Toonen 2011). For the cold-seep dwelling mussel “*Bathymodiolus*” *childressi* and an associated gastropod, *Bathynnerita naticoidea*, larvae were detected in surface currents, suggesting larvae migrate hundreds of meters above the sea floor, allowing greater dispersal in faster surface currents (Arellano et al. 2014). Unfortunately, for the majority of deep-sea coral species, knowledge of larval duration and behavior such as swimming ability is completely absent. In a review of data on pelagic larval durations in deep-sea taxa, a total of 21 species have been characterized. Of these, only three were cnidarian species (Hilário et al. 2015). In fact, knowledge of basic

types of reproduction in deep-sea cnidarians is scarce. For example, of the 615 known deep-sea scleractinian coral species (Cairns 2007), reports on various aspects of reproduction have been ascertained for only 15 species (Waller 2005, Mercier et al. 2011). The structure-forming scleractinian corals *Lophelia pertusa* and *Oculina varicosa* are seasonal broadcast spawning species that release gametes into the water column (Brooke and Young 2003, Waller and Tyler 2005, Brooke and Järnegen 2013). In contrast, hydrocorals in the family Stylasteridae, often an important structural component of deep-sea coral gardens (Stone 2006, Lindner et al. 2008), have a reproductive strategy that involves brooded larvae with a short planktonic duration, which may limit larval dispersal potential (Brooke and Stone 2007). Similarly, *Corallium rubrum*, a precious coral with a wide bathymetric distribution, also broods larvae and releases well-developed, competent larvae (Abbiati et al. 2010). In accordance with brooded larvae, effective dispersal appears restricted (Ledoux et al. 2010a, Constantini and Abbiati 2015), and shallow water populations are genetically structured at a scale of tens of meters (Ledoux et al. 2010b, Abbiati et al. 2010, Aurelle et al. 2011, Aurelle and Ledoux 2013). Many octocorals broadcast gametes into the water column annually, relying on external fertilization and larvae with an extended planktonic development phase (Waller and Baco 2007, Kahng et al. 2011, Mercier and Hamel 2011, Watling et al. 2011, Waller et al. 2014, Nonaka et al., in press, Feehan and Waller 2015), so greater dispersal potential may be expected. Identification of newly-settled individuals is also extremely difficult, and *in situ* measures of recruitment in deep sea corals are limited (Grigg 1988, Thresher et al. 2011, Lacharite and Metaxas 2013).

Traditional methods such as stock assessments or analysis of morphological differences between populations have been used to define conservation management units and potential larval sources. However, *potential* for connectivity between geographically separated populations that do not appear to differ morphologically does not mean active exchange of larvae is occurring. In fact, populations may have been isolated for thousands of years or more yet remain morphologically similar, resulting in genetically differentiated sibling species (see Knowlton 1993). Thus, sampling organisms from different sites and indirectly measuring connectivity using genetic techniques may be the only practical way to understand past and present connections (Palumbi 2003, Shank 2010).

II. Genetic Methods

Use of molecular techniques has changed our view of population structuring and management. Molecular data have demonstrated that a single management unit with a homogeneous, wide-ranging distribution is not necessarily the best management/conservation model (Ayre and Hughes 2000, Swearer et al. 2002, Jones et al. 2005, Almany et al. 2007). For example, the scale over which populations of shallow-water scleractinian corals are differentiated can range from 25 to 7,500 km (Baums 2008), and may involve differentiation with depth (Serrano et al. 2014). A heterogeneous spatial mosaic of multiple units with varying amounts of genetic structure may better describe what is found in nature. Researchers must properly sample geographic populations, consult taxonomists, use appropriate genetic markers (e.g., mitochondrial or nuclear DNA), and consult theoretical models to ascertain the

genetic structure of a species' populations (Pante et al. 2015a).

Over broad geographic scales (e.g., entire ocean basins), mitochondrial DNA markers are often employed to assess connectivity. For most animals, mitochondrial DNA is inherited maternally. Thus, only one copy of each gene exists in an individual. Mitochondrial DNA markers provide some of the most well-known examples of geographic breaks in population connectivity among shallow water marine species such as oysters, horseshoe crabs, and black sea bass along the east coast of Florida (Avisé 1992). Mitochondrial DNA markers have also been useful in identifying closely related (sibling) or morphologically similar (cryptic) species, both of which commonly occur in the deep sea (Rogers 2002). However, mitochondrial DNA evolves at a slow rate in corals (50-100 times slower than most animals) and generally does not provide species-level resolution (France and Hoover 2002, Shearer et al. 2002, Hellberg 2007, McFadden et al. 2011, Baco and Cairns 2012). This slow rate of mitochondrial DNA sequence evolution has impeded studies of connectivity in corals (e.g., van Oppen and Gates 2006, Eytan et al. 2009), where more variable nuclear DNA markers are necessary to assess connectivity.

Realized average dispersal of an organism over its entire life cycle (planktonic larval stage, settlement, maturation) can be estimated from nuclear markers such as microsatellites (Neigel 2002). Microsatellite markers refer to regions of DNA that include adjacent repeats of several nucleotide bases. Microsatellites have a higher mutation rate than mitochondrial DNA, so often reflect connectivity on more recent time scales. However, unlike mitochondrial DNA, nuclear markers like microsatellites are inherited from both parents, so individuals

have two copies of each nuclear gene, called alleles, which are the building blocks that populations utilize to adapt and evolve in changing environments. These alleles may differ in length due to differences in the number of times the nucleotide bases are repeated. When the alleles are identical, they are termed homozygous, different alleles are heterozygous. Often, these population-level molecular markers are species-specific and highly variable. Utilization of rapidly-evolving genetic markers with many alleles allows one to decipher the unique genetic makeup of each individual. Although the initial cost of analysis is higher, results with resolution to the level of individuals and parentage is often worth the expense. Markers with high specificity and variability are utilized to assess family relationships and clonality in organisms, two attributes that complicate the genetic signatures of cold-water coral populations.

One of the most important applications of population genetic data is to determine the level of genetic structuring within and between populations. Genetic structure within a species can range from very weak, where exchange of individuals is common (i.e., high connectivity), to strong genetic structuring, where exchange of individuals is more rare (i.e., low connectivity, moving toward isolation of populations; reviewed by Palumbi 2003, Hedgecock 2007, Cowen and Sponaugle 2009). Genetic estimates of connectivity result from counting differences in DNA sequences or examining the variance in allele frequencies between populations that accumulate when connectivity is low or nonexistent (see below). When genetic structuring is detected, examination of the physical or biological parameters that may be correlated to genetic differentiation may provide clues to the processes that act to determine spatial connections among populations.

Population geneticists also attempt to decipher patterns of genetic connectivity indirectly through the application of theoretical models of population structure (Hedgecock 2007). The stepping-stone model assumes neighboring populations are more likely to exchange migrants amongst themselves than with populations further away (Kimura and Weiss 1964). Thus, genetic distance should increase with geographic distance, populations in closer proximity will be genetically more similar to each other than to populations farther away. This pattern of connectivity, referred to as isolation-by-distance (Wright 1943), creates a highly structured, genetically complex system (Rousset 1997). For example, an isolation-by-distance pattern was confirmed for *Porites lobata* populations inhabiting shallow reefs in the Hawaiian Archipelago (Polato et al. 2010). If an isolation-by-distance pattern of connectivity is detected, estimation of dispersal distances may be biologically meaningful (Rousset 1997, Palumbi 2003).

An indirect measure of the persistence of a metapopulation is genetic diversity. Genetic diversity covaries with the number of patches (sources) that can supply migrants (Maruyama and Kimura 1980, Vrijenhoek 2010). Therefore, estimating genetic diversity within metapopulations is a proxy for the vulnerability of a species to extinction.

III. Connectivity in the Deep Sea

The majority of studies of marine connectivity focus on shallow-water environments, particularly tropical reef fishes (Hixon 2011). Although shallow marine habitats were once considered open systems with ample exchange of larvae over large distances, it is now accepted that local recruitment and small-scale

population structure are common despite the lack of obvious physical barriers (Cowan and Sponagule 2009). Genetic data have suggested similar results for shallow-water corals, in that most recruitment is local, yet occasional long-distance dispersal can occur across tens to hundreds of kilometers (Ayre and Hughes 2000, Miller and Ayre 2008, Gorospe and Karl 2013).

Although less is known about patterns of connectivity in the deep sea, recent studies have suggested common themes. First, similar to shallow populations along coastlines, including many coral species along the Great Barrier Reef (Ayre and Hughes 2004), the stepping stone model may be appropriate for many deep-sea populations, particularly those arranged linearly along continental margins (LeGoff-Vitry et al. 2004, Smith et al. 2004), mid-oceanic ridge axes (Coykendall et al. 2011, reviewed by Vrijenhoek 2010) or linear arrays of seamounts (Samadi et al. 2006).

In contrast, stretches of open ocean that interrupt a linear array of reefs (Ayre and Hughes 2004) or vent populations (Vrijenhoek 2010) may create an effective barrier to dispersal, and connectivity may decrease abruptly, creating regionally isolated populations. Regional differentiation of deep-sea fauna that inhabit continental slope habitats may not be limited to benthic organisms such as corals. Even mobile species, such as fishes (e.g. *Helicolenus dactylopterus* (Aboim et al. 2005), squid (Shaw et al. 1999), scavenging isopods (France and Kocher 1996), and red crabs (Weinberg et al. 2003), show regional structuring (see Rogers 2002). Suggested mechanisms that may prevent panmixia of continental slope species include physical barriers (continents and large expanses of deep water, deep water sills (Coward et al. 2013), or among back-arc

basins (Thaler et al. 2014)), structuring of the water column (density layers), rugged topography (canyons and seamounts) and oxygen minimum zones (Rogers 2002). In addition, species-specific life history strategies, especially related to spawning, may also act to limit exchange of individuals between populations (Rogers 2002).

Shared patterns of species diversity and genetic structuring across unrelated but co-distributed species may indicate that oceanographic features affect connectivity of many species in similar ways (Cunningham and Collins 1998). For example, the deep-sea scleractinian coral species *Desmophyllum dianthus*, as well as two antipatharian species, *Antipathes robillardii* and *Stichopathes variabilis*, exhibited genetic subdivision across large ocean expanses in the southern Pacific Ocean (Miller et al. 2010). Concordance among regional connectivity patterns of these co-distributed species indicates that physical forces (e.g., prevailing currents, eddies, upwelling) may restrict larval dispersal among regions. However, no genetic subdivision was detected for two other coral species (*Solenosmilia variabilis*, *Madrepora oculata*) using the same mitochondrial and nuclear gene regions (Miller et al. 2010). Conversely, using microsatellites instead of mitochondrial DNA, Becheler et al. (in review) identified distinct genetic populations of *Madrepora oculata* among canyons in the Bay of Biscay (Eastern North Atlantic Ocean), yet co-occurring *Lophelia pertusa* were panmictic. Clearly, no generalized connectivity pattern applies to all coral species.

A factor that may uniquely influence connectivity among deep-sea organisms is depth. Pronounced physiological gradients occur as depth increases, which could result in locally adapted populations and enhanced

genetic differentiation (Rogers 2002, Zardus et al. 2006). This concept, known as the depth-differentiation hypothesis (Rex and Etter 2010), suggests that the divergent selection across environmental gradients may cause population differentiation, leading to new and/or cryptic deep-sea species. Depth-related divergence has been identified in molluscs (e.g. Chase et al. 1998, Etter et al. 1999, Goffredi et al. 2003, Etter et al. 2005, Zardus et al. 2006, Jennings et al. 2013), polychaetes (Lundsten et al. 2010, Schüller 2011, Cowart et al. 2014), amphipods (France and Kocher 1996, stylasterid corals (Lindner et al. 2008), primnoid octocorals (Baco and Cairns 2012), and the red coral *Corallium rubrum* (Constantini et al. 2011). In other deep-sea corals, limited vertical larval dispersal has been suggested the solitary coral *Desmophyllum dianthus*, a scleractinian coral with a cosmopolitan distribution. Genetic differentiation with depth in *D. dianthus* was consistent with the stratification of deep water masses that entrain larvae and do not allow mixing among depth strata (Miller et al. 2011). In a study that included three species of octocorals in the Gulf of Mexico, an ecological niche model revealed little overlap among *Callogorgia* species occupying different depths (Quattrini et al. 2013). The depth differentiation hypothesis was tested of these species, *Callogorgia delta*, using microsatellite data, and isolation by depth was confirmed (Quattrini et al. 2015). Rex et al. (2005), using deep-sea molluscan fauna with bathyal and abyssal distributions as examples, postulate that the abyssal environment may create population sinks due to a decrease in organic carbon influx from more productive coastal systems. These isolated populations rely on bathyal populations for immigrants. Conversely, nine genetic breaks were detected in the cosmopolitan deep-sea

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REFERENCE	SPECIES	REGION	MARKERS	CONNECTIVITY	IBD
Eytan et al. 2009	<i>Oculina varicosa</i>	WNAntlantic	4 nuclear DNA genes	Depth structured	No
Thoma et al. 2009	6 octocorals, 2 antipatharians	WNAntlantic, NE Seamounts	mtDNA	No structuring, high connectivity	NA
Cho and Shank 2010	<i>Asteroschema clavigerum</i> <i>Ophiocreas oedipus</i> <i>Ophioplinthaca abyssalis</i> <i>Ophioplinthaca chelys</i>	WNAntlantic, NE Seamounts	2 mtDNA genes	Regional seamount structure, depth	Yes
Morrison et al. 2011	<i>Lophelia pertusa</i>	North Atlantic	9 microsatellites	Regional structure, moderate connectivity within regions	Yes, broad scale
Baco and Shank 2005 Baco et al. 2006	<i>Corallium lauuense</i>	Central Pacific	3-6 microsatellites	High connectivity, structure between sites and depths	No
Baco and Cairns 2012	Several <i>Narella spp</i>	North Pacific	6 mtDNA markers	Narrow geographic and depth ranges for haplotypes	NA
Herrera et al. 2012	<i>Paragorgia arborea</i>	North Pacific, South Pacific, North Atlantic	7 mtDNA genes	Regional structure	NA
Quattrini et al. 2015	<i>Callogorgia delta</i>	Gulf of Mexico	10 microsatellites	Depth structured	Yes, depth > distance

Table 1. Studies examining connectivity among deep-sea corals and/or deep coral communities in U.S. waters.

amphipod *Eurythenes gryllus*. In this instance, higher diversity was observed at abyssal rather than bathyl depths, thus reflecting a pattern contrary to the depth-differentiation hypothesis (Havermans et al. 2013). Clearly, environmental factors associated with depth may create important abiotic gradients that may influence population structuring in the deep sea (Quattrini et al. 2015).

IV. Connectivity Among Deep-Sea Corals in U.S. Waters

IV.1. North Atlantic Ocean

Genetic methods were used to assess connectivity patterns in several North Atlantic deep-sea coral species (Table 1). In the first of these studies, connectivity among shallow and deep populations of the structure-forming coral *Oculina varicosa* was examined using three nuclear DNA sequence markers (Eytan et al. 2009). *Oculina varicosa* occurs most commonly at shallow depths (< 30 m). However, azooxanthellate colonies grow at 70 to 100 m depth along the *Oculina* Banks off the Florida east coast (Reed 2002). Despite Federal protection, the *Oculina* Banks have been negatively impacted by illegal trawling and dredging (Reed et al. 2007). The *Oculina* Banks population was found to be distinct from shallow populations; therefore, depth was considered an important factor structuring the pattern of connectivity in *O. varicosa* (Eytan et al. 2009).

Lophelia pertusa, a structure-forming coral species commonly found on the continental slope off the southeastern U.S. coast (Ross and Nizinski 2007) and Gulf of Mexico (Brooke and Schroeder 2007), has a nearly cosmopolitan distribution, suggesting substantial dispersive ability. *Lophelia pertusa*

is a broadcast spawner that was originally thought to produce non-feeding larvae (Waller and Tyler 2005). Yet a recent study suggests larvae may feed and actively swim upwards during the first weeks after fertilization, a behavior that may allow larvae to rise above the benthic boundary layer and promote advection in stronger currents (Larsson et al. 2014). Swimming behavior as well as an estimated three to five week larval duration imply high dispersal potential. However, the spatial scales that *L. pertusa* larvae travel remains unknown, making accurate predictions of realized larval dispersal challenging. Nine microsatellites were used to examine patterns of genetic connectivity across a large portion of the geographic range of *L. pertusa* in the North Atlantic Ocean (Morrison et al. 2011). Four distinct genetic groupings corresponding to ocean regions were identified: Gulf of Mexico, coastal southeastern U.S., New England Seamounts, and eastern North Atlantic Ocean (Figure 2). It is known that reproductive timing is offset between the eastern North Atlantic (Waller and Tyler 2005) and Gulf of Mexico (Brooke et al. 2007) *L. pertusa* populations. Whether or not regionally isolated *L. pertusa* populations represent cryptic species will require further morphological examination and biological evidence. Interestingly, similarities exist between zoogeographic patterns of deep-sea scleractinian corals (Cairns and Chapman 2001) and regional *L. pertusa* genetic differentiation (Morrison et al. 2011), suggesting that similar mechanisms (see above) may constrain coral larvae within regions.

Although the populations of *L. pertusa* at the New England seamounts occur in a geographic location that could be a corridor, or stepping stone, for connectivity across the Atlantic Ocean, the seamount populations

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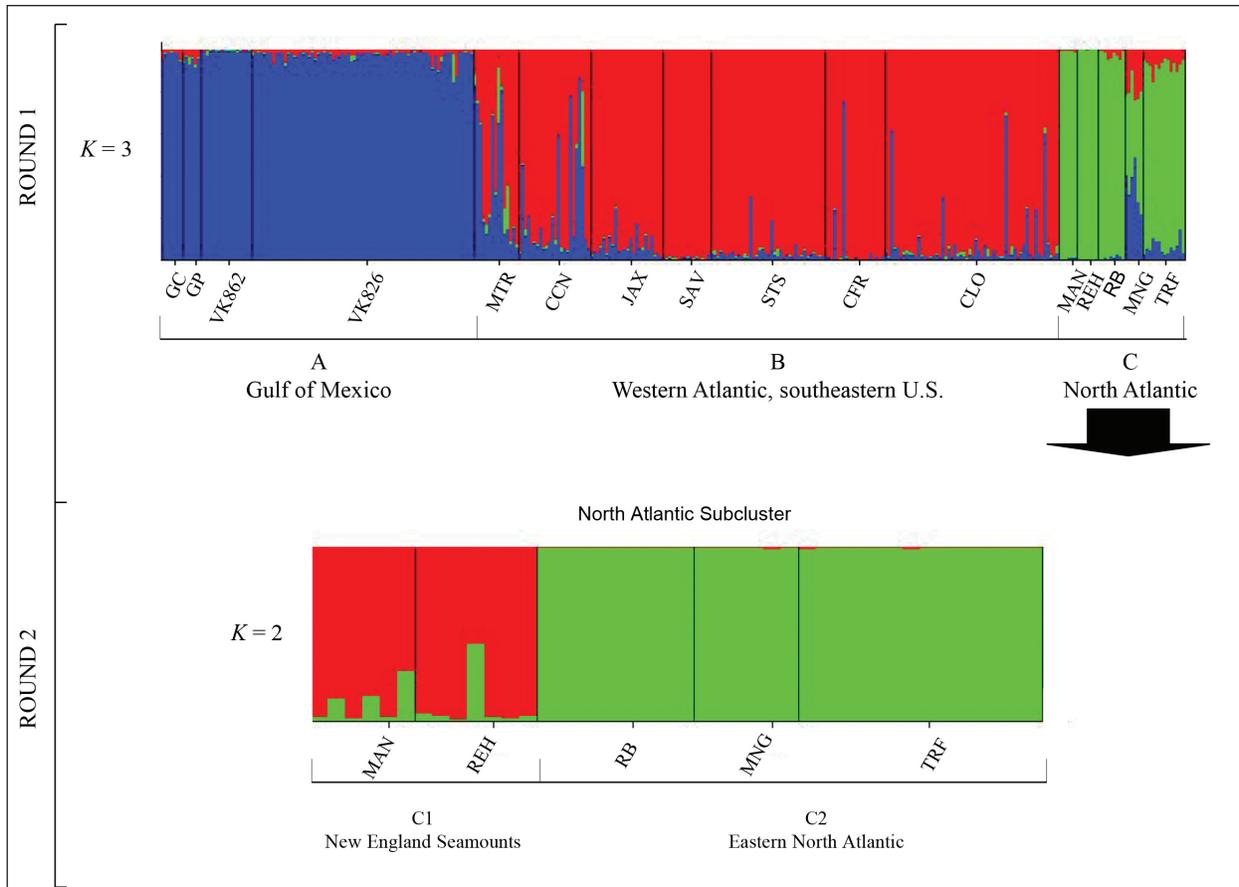


Figure 2. Probability of assignment of *Lophelia pertusa* individuals, represented by colored vertical bars, to four groups based upon multi-locus genotypes using the program STRUCTURE. Populations are arranged from west (left) to east (right). The top bar (round 1) represents an initial run including all *L. pertusa* samples. The lower bar represents additional structuring between New England Seamounts and Eastern North Atlantic populations detected during a subsequent run of STRUCTURE. (Reprinted from Morrison et al. 2011, *Conservation Genetics*; 37).

were the most genetically differentiated based upon microsatellites, suggesting little connectivity (Morrison et al. 2011). The seamount populations appeared more genetically similar to populations from the eastern rather than western North Atlantic Ocean, despite occurring in closer proximity to the latter. These seamount populations occur deeper (1418-1679 m) than other populations sampled (140-740 m) and therefore differing water masses and circulation patterns may act as a barrier to gene flow.

For North Atlantic Ocean *L. pertusa* populations, a positive correlation between genetic and geographic distance was detected at broader scales (thousands of km), but not at smaller scales (Morrison et al. 2011). Since regional breaks in connectivity were also detected, deductions regarding dispersal distances may be compromised due to the likely violation of the stepping-stone model assumption of on-going dispersal at these large scales (Slatkin 1993, Garnier et al. 2004). However, results suggest moderate connectivity within each of the regions. A

previous study of *L. pertusa* in the eastern North Atlantic Ocean also reported moderate connectivity (genetic cohesion) among European continental margin populations and no correlation between genetic and geographic distance (Le Goff-Vitry et al. 2004). Levels of both inbreeding and asexual reproduction (clones) varied among European margin *L. pertusa* populations, suggesting that most dispersal is spatially restricted, yet occasional long-distance dispersal is adequate to maintain genetic cohesion (Le Goff-Vitry et al. 2004). While both studies detected genetic structuring (i.e., decreased connectivity) between continental slope and Norwegian fjord *L. pertusa* populations in the eastern North Atlantic, results from Morrison et al. (2011) suggest the magnitude of differentiation is less than that observed across the North Atlantic Ocean.

Lophelia pertusa populations surveyed in both the eastern and western North Atlantic Ocean using microsatellites have shown heterozygote deficiencies (Le Goff-Vitry et al. 2004, Morrison et al. 2011, Dahl et al. 2012). Similarly, heterozygote deficits have been detected in the majority of population genetic studies of corals (Ayre and Hughes 2000, van Oppen and Gates 2006, Selkoe and Toonen 2006), including cold-water corals (Baco and Shank 2005, Baco et al. 2006). Occurrence of heterozygote deficits in nature is often explained as a violation of the concept of the 'ideal population' assumed by the Hardy-Weinberg principle. For instance, a subset of the population could contribute the most genetic material to the next generation (non-random mating). Studies have shown a propensity for clonal reproduction via fragmentation in most *L. pertusa* populations surveyed (Le Goff-Vitry et al. 2004, Morrison et al. 2011, Dahl et al. 2012).

Clonal reproduction can cause heterozygote deficits due to deviation from random mating (Dahl et al. 2012, van Oppen et al. 2008). In fact, asexual reproduction via fragmentation may play a key role in the establishment and maintenance of deep *L. pertusa* reefs (Dahl et al. 2012). For example, few genetic individuals become dominant at a reef site and skew opportunities for mating. Additionally, the lifespan of a genetic individual may be quite long (thousands of years; Dahl et al. 2012), therefore, this life history trait may be important to both estimates of connectivity and to the evolution of the species.

Seamounts are hypothesized to be locations of isolation in the deep-sea, resulting in high levels of speciation and endemism (e.g. Hubbs 1959, Rowden et al. 2010, Pante et al. 2015b). Three studies (Thoma et al. 2009, Cho and Shank 2010, Herrera et al. 2012) have addressed connectivity along the New England and Corner Rise Seamounts. Thoma et al. (2009) investigated isolation among individual seamounts by testing the hypothesis that corals occurring at isolated seamounts would possess unique mitochondrial DNA haplotypes. Variability in the mitochondrial mismatch repair gene homolog (*mutS*) was assessed for five octocoral genera. Nine markers for antipatharians as well as an intergenic spacer for bamboo corals were also incorporated into the data set.

The Thoma et al. (2009) study found four haplotypes unique to the seamounts, as well as two haplotypes from the adjacent margin that were widespread, consistent with the possibility of seamounts being hotspots for divergence of species. A caveat of this work is that the unique haplotypes discovered at the seamounts were not necessarily the result of endemism, but could be due to small

sample sizes. This work, however, is based on the assumption that *mutS* haplotypes were species-specific. Subsequent work has shown this is not the case. Rather, some species of octocorals have multiple haplotypes for *mutS*, which can lead to underestimating species ranges, while other *mutS* haplotypes are shared between multiple species, resulting in overestimating species ranges (McFadden et al. 2010, McFadden et al. 2011, Baco and Cairns 2012, Pante et al. 2015b). These same studies show that only about 50% of species could be resolved using the *mutS* marker. Thus the single-marker approach of Thoma et al. (2009) likely does not provide sufficient power to resolve the connectedness of the New England and Corner Rise seamounts at the species level.

In contrast, data from seven mitochondrial gene regions and nuclear genetic variants of the deep-sea bubblegum coral *Paragorgia arborea* revealed basin-wide and global patterns of genetic variation correlated with historical migrations and connectivity from the Western Pacific into the Atlantic (Herrera et al. 2012). Prior to this study, diversity throughout the entire known distribution of a cold-water coral species had not been evaluated. Herrera et al. (2012) utilized mitochondrial and nuclear genetic variants in a phylogeographic context to examine the compatibility of *P. arborea* with the genealogical-phylopecies concept by examining specimens collected over its known distribution. The multi-marker use demonstrated that the global morphospecies *P. arborea* can be defined as a genealogical-phylospecies hosting differing levels of connectivity around the world's oceans. Global genetic variation among populations of this species revealed significant basin scale differences. These phylogeographic data suggest a scenario in which *P. arborea*

originated in the North Pacific, possibly in the Western North Pacific, followed by colonization of the South Pacific and spreading eastward around the Southern Hemisphere in a stepping stone fashion (possibly via the Antarctic Circumpolar Current). The colonization of the North Atlantic seems to have occurred through a more recent dispersal event from the South Pacific, via the Central American Seaway, or from the South Atlantic. Notable is that despite the finding of significant geographic variation over the geographic range, no significant correlation with depth was observed.

A study by Cho and Shank (2010) demonstrated the impact host-specific symbiotic relationships may have on the genetic connectivity of fauna associated with cold-water corals. Deep-sea corals provide habitat for many species that have developed symbiotic relationships with varying degrees of specificity to their host corals (Shank 2010, Buhl-Mortensen et al. 2010). The co-evolution of host-associate relationships may affect the genetic connectivity of these coral associates. Cho and Shank (2010) studied the patterns of dispersal and genetic connectivity of four brittle star species (*Asteroschema clavigerum*, *Ophiocreas oedipus*, *Ophioplinthaca abyssalis* and *Ophioplinthaca chelys*; Figure 3) that display differing levels of associative specificity to deep-sea coral hosts inhabiting the New England and Corner Rise seamounts.

Analyses of two mitochondrial markers, mt16S and mtCOI, revealed species-specific genetic differentiation based on geography and depth. *Asteroschema clavigerum* and *O. oedipus* showed significant isolation by distance, significant genetic differentiation by depth, and predominantly westward historical migration. *Asteroschema clavigerum*

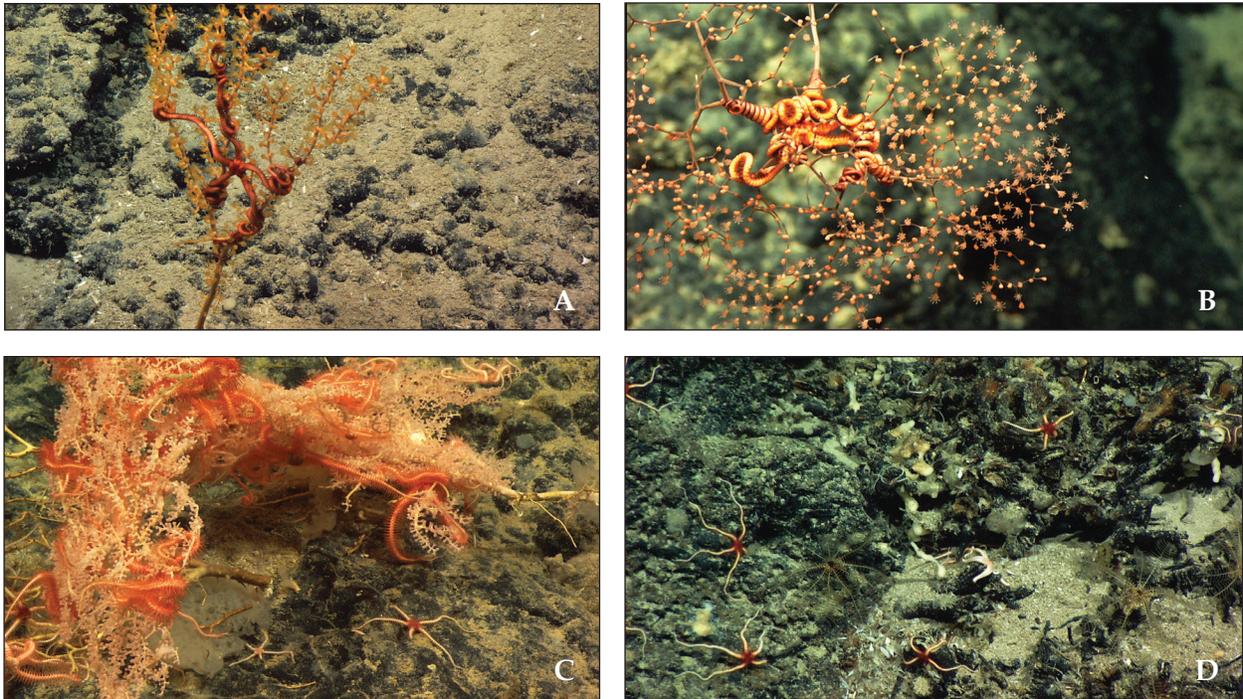


Figure 3. Images of four brittle star species studied by Cho and Shank (2010). A) Brittle star *Asteroschema clavigerum* found on the deep-sea coral *Paramuricea* sp. B) Brittle star *Ophiocreas oedipus* found on the deep-sea coral *Metallogorgia melanotrichos*. C) Brittle stars *Ophioplinthaca abyssalis* found on the deep-sea coral *Candidella imbricate*. D) Brittle stars *Ophioplinthaca chelys* found on the sea floor. Image credit: WHOI; DASS 2005 Expedition; IFE; NOAA OE.

had significant genetic differentiation by geographic region. In contrast, *O. abyssalis* and *O. chelys* displayed predominantly eastward historical migration and *O. chelys* displayed significant genetic differentiation within individual seamounts. The patterns of genetic differentiation shared by *A. clavigerum* and *O. oedipus* may be correlated with species-specific host specificity and dispersal strategies. Both of these species have seemingly obligate symbiotic relationships to their specific coral hosts and are broadcast spawners, while the other two species studied, *O. abyssalis* and *O. chelys*, have lower or no fidelity to their coral hosts and are potentially brooders.

IV.2. North Pacific Ocean

Although scleractinian reefs are not common in the North Pacific Ocean, dense deep-sea coral assemblages, dominated by octocorals and antipatharians, are found throughout the region (Baco 2007, Hourigan et al. 2007). Despite the high diversity and abundance of corals, population genetics analysis of only one species has been published. *Hemicorallium laauense* (= *Corallium laauense*), a commercially important octocoral in the family Coralliidae, harvested periodically as part of the precious coral fishery (reviewed in Grigg 2002), is numerically dominant in the Hawaiian Archipelago at 350-575m depth (Parrish and Baco 2007, Baco 2007). *Hemicorallium laauense* appears to spawn with a periodic or quasi-continuous reproductive strategy (Waller and Baco 2007).



Because of the relatively linear nature of the Hawaiian Archipelago, one would expect a classic isolation-by-distance signature in the genetic data for most species. However, results from an analysis of three microsatellite loci in *H. laauense*, collected from eight sites in the Main Hawaiian Islands and southern end of the northwestern Hawaiian Islands, indicated no isolation-by-distance pattern (Baco and Shank 2005). Instead, results indicate that the scale of genetic structure on isolated features such as oceanic islands and seamounts may be more complex than a simple stepping-stone model. For example, the deepest site, located off Kauai in the middle of the sampling area, was quite different genetically compared to the majority of sites sampled during the study. Also, there was significant variation within the continuous Makapu'u bed (on the scale of 1.6 km) off the Island of Oahu. The fairly high heterozygote deficiency found for this species based on six microsatellite markers (Baco and Shank 2005, Baco et al. 2006) could indicate a high degree of inbreeding for this species, implying significant isolation for each of the precious coral bed locations investigated, with only occasional long distance dispersal events. These results suggest connectivity within and between each feature on or each location along a seamount chain should be assessed when considering any management actions.

Analyses based upon mitochondrial DNA also provide some insight into connectivity along North Pacific seamounts. Previous studies of seamount octocorals indicated widely distributed mitochondrial haplotypes and counter the idea that seamounts may be isolated (Smith et al. 2004, Thoma et al. 2009). However, each of these studies cautions that mtDNA markers were not morphologically ground-truthed to determine the level of genetic variation which corresponds to a species. A recent study of the octocoral genus

Narella (Family Primnoidae) examined the variability of six mtDNA regions relative to species designations in this genus (Baco and Cairns 2012). The results of this study indicated that the markers used in previous studies could not distinguish individuals at the species level (*mutS*) and two markers (indel regions) could not distinguish between genera (Smith et al. 2004) based on mtDNA haplotypes. Thus, the fact that haplotypes were widespread is not sufficient evidence to disprove isolation of seamount features. Using all six mtDNA markers on specimens collected on North Pacific seamounts, the results of the *Narella* study indicate that geographic and bathymetric ranges of seamount species may be much narrower than previously thought.

V. Future Directions

Whereas the examples discussed above provide insights into patterns of connectivity for several abundant and important deep-sea coral species in U.S. waters, much work remains before we can achieve a fundamental understanding of the factors that control connectivity among coral species and their diverse associated fauna. Several specific research questions that may guide future studies of connectivity among deep-sea corals are suggested below.

V.1. How Far do Larvae of Deep-Sea Corals and Associated Organisms Disperse?

A basic understanding of distributions of deep-sea coral species and associated fauna, coupled with a thorough taxonomic evaluation, is necessary to address this research question (see Pante et al. 2015a). Although general ranges for many deep-sea coral species are known, the need exists to

fine-tune estimates and fill in information gaps by visiting unexplored areas. Exploratory cruises are necessary to locate populations, assess abundances, and collect samples. Success in locating and sampling deep-sea corals and associated organisms during exploratory cruises will depend upon access to deep-submergence technologies (see below). Additionally, such explorations may be guided by predictive biophysical modeling, which may help locate where previously unknown coral habitats occur (e.g. Yearsley and Sigwart 2011). Predictive modeling involves methods that produce distribution maps from limited sampling data, as interpreted through remote sensing information such as multibeam bathymetry, substrate and geomorphology, rugosity, slope and aspect (e.g., Howell et al. 2011) and/or aspects of the environmental tolerances of corals compared with physical, chemical and biological variables at the geographic locations being studied (Davies et al. 2008, Guinotte et al., this volume)). The effective use of biophysical models for deep-sea organisms is hampered by knowledge gaps in both physical and biological parameters (Hilário et al. 2015

While sampling deep-sea organisms can be labor intensive and expensive, obtaining sufficient numbers of individuals per population for statistical testing has strongly impeded progress to date. Need for adequate numbers of samples is regarded as essential and of critical importance. A balance between adequate sampling of local populations and sampling broadly throughout the geographic range of the species is imperative (Pante et al. 2015a). Therefore, funding agencies and science parties need to appreciate the value of connectivity studies and dedicate dive time specifically for sampling spatially structured populations. Much can be gained through collaborative efforts in large-scale and multi-

species connectivity studies if adequate time for intensive sampling of individual species is included in the sampling plan.

With the advance of new genetic tools and the unknown scales of dispersal for almost all deep-sea corals and their symbionts, fine-scale (spatial and temporal) studies are now needed. For example, genetic structure was found at very small spatial scales (within a reef) but disappeared or became negative at larger scales in Hawaiian *Pocillopora* corals (Gorospe and Karl 2013). Clonal reproduction through fragmentation in scleractinian corals may be key to extreme longevity of a genetic individual (clone), and may skew chances for reproduction to a few individuals (Dahl et al. 2012). Therefore, sampling should address fine-scale structuring adequately. The feasibility of such a sampling scheme has been demonstrated (Becheler et al., in review). Larger sample sizes and additional markers are necessary to obtain the statistical power necessary to distinguish small but important genetic distinctions (Waples 1998, Hedgecock 2007).

V.2. Can Larval Dispersal Distances be Accurately Estimated Given Current Knowledge of Early Life Histories?

Early life history traits, such as timing and potential seasonality of reproduction, reproductive output and success, planktonic duration, and recruitment, all influence connectivity (e.g. Underwood and Fairweather 1989, Rosser 2015). Reproductive periodicity, larval type and behaviors are fundamental processes that need further investigation (Hilário et al. 2015). In the few species that have been studied, nearly all modes and patterns of reproduction have been observed

(Patarnello et al. 2007, Metaxas and Kelly 2010, Mercier et al. 2011). Thus, making predictions on dispersal, based upon taxon, depth, or location, is extremely difficult.

Assessing patterns of connectivity among organisms associated with deep-sea coral habitats will expand understanding of the functioning of and potential sensitivities to disturbance of these ecosystems. By comparing patterns of genetic connectivity between different species within the same habitat, we gain insight into what drives migration and dispersal in these ecosystems (community genetics). Contrasting patterns of population structure observed among species within the same habitat indicates different life histories are driving resultant dispersal patterns (i.e., vagile vs sessile, lecithotrophic vs planktotrophic larvae) whereas similar patterns of population structure among species within the same habitat indicate larger forces, such as deep ocean current circulation that entrain larvae, are acting on organisms similarly. For example, Samadi et al. (2006) examined connectivity among populations of several squat lobster species and two gastropod species along the Norfolk ridge seamounts. Results suggested that connectivity is restricted only for species with limited dispersal ability. Thus, life history is an important factor shaping connectivity patterns along this seamount chain.

V.3. To What Extent do Patterns of Connectivity Relate to Hydrodynamics?

For shallow-water marine taxa, integration of genetic, biological, geographic and hydrodynamic data into dispersal models has provided both estimates of connectivity as well as descriptions of physical forces that likely shape connectivity patterns (Manel et

al. 2003, Galindo et al. 2006, Cowen et al. 2006, Baums et al. 2005, Baums et al. 2006, Werner et al. 2007, Mokhtar-Jamaï et al. 2011, Foster et al. 2012). Hydrodynamic patterns surrounding deep-sea coral areas are less known (see Hilário et al. 2015, for review). However, physical data are now being collected in some deep-sea regions through the deployment of instrumentation that sequentially collects environmental data over either short (autonomous underwater vehicles) or long periods of time (benthic landers; e.g. Davies et al. 2010, Yearsley et al. 2011). Integration of ocean circulation and larval transport models (based upon laboratory tested larval durations of seven deep-sea invertebrates) exemplified the various patterns of dispersal possible (Young et al. 2012). General conclusions from this study were that most larvae are retained in the same geographic location as adults, but when there is net transport of larvae out of an area, it is unidirectional in an eastward and northward trajectory in Intra-American seas (Young et al. 2012). The combination of genetic connectivity and hydrodynamic data at key time periods (i.e., coral spawning) should allow for better precision in predictive modeling of both dispersal potential and coral presence.

V.4. What Research Tools May be Useful for Studies of Connectivity in the Deep Sea?

Continued development of genetic tools is necessary to fill large knowledge gaps regarding evolutionary processes that shape diversity in the deep sea. Through the application of genetic techniques, patterns and limits of species distributions as well as patterns of dispersal, migration, recruitment and clonality can be described. Choosing the most appropriate genetic tools is project-

specific, dependent upon the question driving the research. For poorly characterized taxa, DNA sequence data is necessary to identify and refine species boundaries and relationships between closely related taxa prior to further analyses (Knowlton 2000). For example, examination of morphological and phylogenetic data is necessary prior to population genetic analyses for most octocoral species (McFadden et al. 2010). Given the prevalence of regional and bathymetric cryptic species (France and Kocher 1996, Etter et al. 1999, Etter et al. 2005, Chase et al. 1998, Vrijenhoek 2009, Miller et al. 2010, Miller et al. 2011, Puillandre et al. 2011, Mantelatto et al. 2014, Pante et al. 2015a), it is likely that the number of deep-sea species has been underestimated (Rogers 2002). Broad-scale sampling and DNA sequencing of few samples can address the taxonomy as well as provide a first order understanding of relationships among geographically distant populations. Adequate sampling, plus simultaneous molecular and traditional systematic investigations may eventually produce more accurate species lists and better evolutionary descriptions of the evolutionary relationships among them (Vrijenhoek 2009, Pante et al. 2015a). These kinds of results would provide the foundation for future population genetic studies. Sampling of this nature should be incorporated into cruise objectives. Additionally, continued database development, promotion of data and sample sharing, plus synthesis and collaboration, should allow for advancements in understanding (McClain and Hardy 2010).

Inexpensive production of large volumes of sequence data for any organism is now possible using next-generation sequencing technologies (NGS). These new sequencing technologies offer exciting prospects for marker development in deep-sea

coral taxa. Researchers using NGS can identify microsatellites more quickly and inexpensively (e.g. Coykendall and Morrison 2013, Morrison et al. 2015). Additional types of molecular markers, such as single-copy nuclear genes (e.g. Concepcion et al. 2008), and single-nucleotide polymorphisms (SNPs, e.g. Baird et al. 2008), may now be developed without prior knowledge of the genome (Reitzel et al. 2013). SNPs are often numerous (hundreds to thousands) and may provide higher genome coverage than microsatellites (tens of markers). The utility of SNPs for delimiting recalcitrant species of octocorals in the genera *Chrysogorgia* (Pante et al. 2015c) and *Paragorgia* (Herrera and Shank 2015) was recently demonstrated. Whether or not differentiation is detected using neutral genetic markers as discussed thus far, populations may be adapted to local environmental conditions. By sequencing coding regions of the genome, genes that may underlie functional variation can be identified and surveyed through gene expression analyses (e.g. Vera et al. 2008). As such, advances in both sequencing technologies and statistics for population genomics may allow researchers to identify genome-wide signatures of adaptation (Baums 2008, Ledoux et al. 2015). Collection of environmental data that may be correlated with differences in gene expression will add value to population genomic studies and may help to identify the mechanisms that generate and maintain diversity.

For certain deep-sea coral associates, chemistry of calcified structures (e.g., fish otoliths and molluscan statoliths) can be used to assess natal origins of individuals and help define geographic scale of dispersal and connectivity. These metabolically inert structures record the chemistry of the environment in which the animal lives.



Natural tags are derived from variation in environmental conditions, including temperature, salinity, dissolved oxygen, and other chemical parameters. If the environmental chemistry is distinct, then these chemical tags provide a record that chronicles spatial separation during spawning, and differences between populations (Campana et al. 1994). While connectivity in shallow-water environments has been addressed using this technique (Thorrold et al. 2007, Eldson et al. 2008), application in the deep sea has been limited to a few studies focused on stock assessments of commercially exploited fishes (Hauser and Carvalho 2008). Combined approaches using microsatellite markers and otolith chemistry can help assess fine scale genetic structure in deep-sea fishes, because these tools document both the ecological and evolutionary timescales appropriate for assessing dispersal (Carlsson et al. 2011)

Working in the deep-sea environment is challenging and costly, and the advancement of connectivity research and exploration is intimately tied to advancements in deep-submergence technologies. Future technological achievements will be those that comprehensively expand our ability to characterize factors fundamental to understanding connectivity, including refining distributions of subpopulations and habitats, obtaining co-located oceanographic data over relevant temporal and spatial scales of connectivity, confirming the presence of fauna and habitat availability, and collecting sufficient numbers of population-level samples for taxonomy and connectivity studies. Improved AUVs offer long-range multi-sensor platforms for spatially-expansive survey coverage, precise dynamic navigation, fine-scale bathymetric mapping, high-resolution photographic and chemical laser imaging (e.g., detecting

species-specific chemicals secreted by corals), coupled with coincident oceanographic data. The use of remotely-deployed cameras (e.g., drop cameras and towed camera sleds) allows for rapid ground-truthing of habitats and targeting of prime habitat for further observation, exploration, and sampling using Remotely Operated Vehicles (ROVs) and/or submersibles. Development of novel sampling gear for ROVs and submersibles that allows many discrete samples to be collected per dive will increase sampling resolution and extent. Lastly, strategically-placed long-term monitoring instrumentation, including time-lapse cameras, oceanographic data samplers, plankton samplers and non-lethal sample collection devices, will help resolve long-term oceanographic patterns as well as provide insights into species behaviors and larval transport. Advancing technological capabilities, including autonomous oceanographic characterization of seafloor habitats, expands our fundamental understanding of benthic processes and their link to coral community connectivity.

VI. Conclusions

Understanding connectivity and the processes that influence connectivity can enhance the conservation of deep-sea coral diversity through science-based stewardship. Connectivity through exchange of larvae among populations should be one of the factors considered during the planning and design phases of deep-sea coral protection areas. Combining estimates of genetic connectivity with physical oceanographic data will lead to a better understanding of processes that underlie larval dispersal and, therefore, connectivity. Population connectivity data among deep-sea coral populations is slowly becoming available. However, more work is needed and research



must continue as scientists and managers work toward protecting and conserving these ecologically valuable ecosystems.

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