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Biogeography and Population Connectivity of Coral Reef Fishes

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1. Introduction

Most fundamentally, the distribution of populations and species is a function of both habitat availability and dispersal ability. Understanding the patterns that result from the interaction of these factors is one of the central aims of ecology. It has long been recognized that populations are not evenly distributed throughout the entire geographic range of the species. Populations occupy spatially distinct patches of suitable habitat that are separated from each other by areas of unsuitable habitat. Depending on factors such as the distance between populations, the nature of the intervening environment, and the relative mobility of the organisms in question, areas of unfavorable habitat may or may not prevent movement of individuals among patches. Given a long enough period of isolation between populations of the same species, speciation or local extinction may result. The degree of connectivity among populations therefore has major ecological and evolutionary implications.

Though the implications of connectivity have long been acknowledged and explored in terrestrial organisms, variable connectivity patterns are only beginning to be recognized as an important driver of present-day population dynamics in the marine realm. It had long been assumed that, due to the lack of visible barriers and the presumed ability of larvae to passively disperse great distances by riding ocean currents, marine organisms dispersed freely and had high levels of population connectivity throughout their ranges. Recent studies in coastal habitats, however, have revealed that the larvae of many coral reef fish species actually settle much closer to their natal reefs than previously thought (Almany et al., 2007; Jones et al., 1999; Kingsford et al., 2002; Planes et al., 2001, Swearer et al., 1999; Taylor & Hellberg, 2003). Similarly, population structure has been found in pelagic species such as cod (Bentzen et al., 1996; Ruzzante et al., 2000) and tuna (Block et al., 2005; Carlsson et al., 2004).

The existence of patchy marine populations, especially if the patches are not connected by migration or dispersal, has enormous implications for biodiversity conservation and management. For instance, isolated populations are more prone to extinction than are more connected ones (Munday, 2004). In this chapter we present an overview of the distribution and population connectivity patterns of coral reef fishes and the methods that have been used to quantify them. We argue that widespread variability in predicted and observed patterns can be explained via the interaction between reef fish life history traits and oceanographic conditions. We emphasize throughout the importance of understanding the

interactions among evolutionary, ecological, and physical processes in structuring contemporary distribution and dispersal patterns. Finally, we address how a better knowledge of connectivity among reef fish populations holds the potential to dramatically improve management and conservation of threatened coral reef ecosystems.

2. Coral reef fish biogeography: The link between evolutionary and ecological processes

Biogeography, or the study of the distribution of organisms in space and time, asks which species occur where, and why or why not (MacArthur and Wilson, 1967). The answers to these questions are complex, since contemporary distribution patterns of organisms reflect biological and physical processes operating at multiple spatial scales, on both evolutionary and ecological time scales. We focus here on the study of coral reef fishes, specifically the ten families that are considered to be characteristic of modern coral reef ecosystems: Acanthuridae (surgeonfish), Apogonidae (cardinalfish), Bleniidae (blennies), Carangidae (jacks), Chaetodontidae (butterflyfish), Holocentridae (squirrelfish), Labridae (wrasses), Mullidae (goatfish), Pomacentridae (damselfish and clownfish), and Scaridae (parrotfish) (Bellwood, 1996). Coral reefs have existed in some form since the Ordovician period (Wood, 1999), and the biogeographic and taxonomic patterns observed in coral reef fish families today reflect a long and complex history of geological, oceanographic, and biological interactions (Bellwood & Wainwright, 2002). The contemporary distribution and population structure of coral reef fishes appear to be similarly mediated by both geography and life history. In our subsequent discussion of emergent biogeographic and taxonomic patterns, we use the term "reef fish" to refer specifically to tropical coral reef fish.

2.1 Temperature controls the distribution of suitable habitat

The global dispersal of coral reef fishes is broadly controlled by the availability of suitable habitat, which is dictated by the shape of the latitudinal temperature zone around the Equator. The Tropical Zone (Figure 1) was formed by dramatic cooling at high latitudes long ago in the Earth's geological history, and it remains constrained today by the flow of major ocean currents (Briggs, 2007). Oceanography also influences reef fish distributions within the confines of this tropical zone. On the western sides of the Atlantic and Pacific Ocean basins, the North and South Equatorial currents turn toward higher latitudes, bringing warm water and tropical organisms with them. On the eastern sides of the ocean basins, however, the major currents turn toward the tropics, transporting colder water from higher latitudes toward the Equator. This oceanographic pattern ensures that the western regions of each basin have a larger area of tropical marine habitat (Briggs, 2007), and therefore greater species diversity, than do the eastern regions.

The Tropical Zone (TR) defines the latitudinal availability of suitable tropical habitat. Within this temperature zone, several major faunal boundaries have contributed to marine speciation events in the past and continue to act as barriers to reef fish dispersal in the present: the Red Sea land bridge, the Indo-Pacific Barrier, the Eastern Pacific Barrier, and the Isthmus of Panama. Together with temperature restrictions, these dispersal barriers have produced five longitudinal biogeographic regions: the Indian Ocean, the Indo-West Pacific, the Eastern Pacific, the Western Atlantic, and the Eastern Atlantic (Bellwood & Wainwright, 2002; Briggs, 2007).
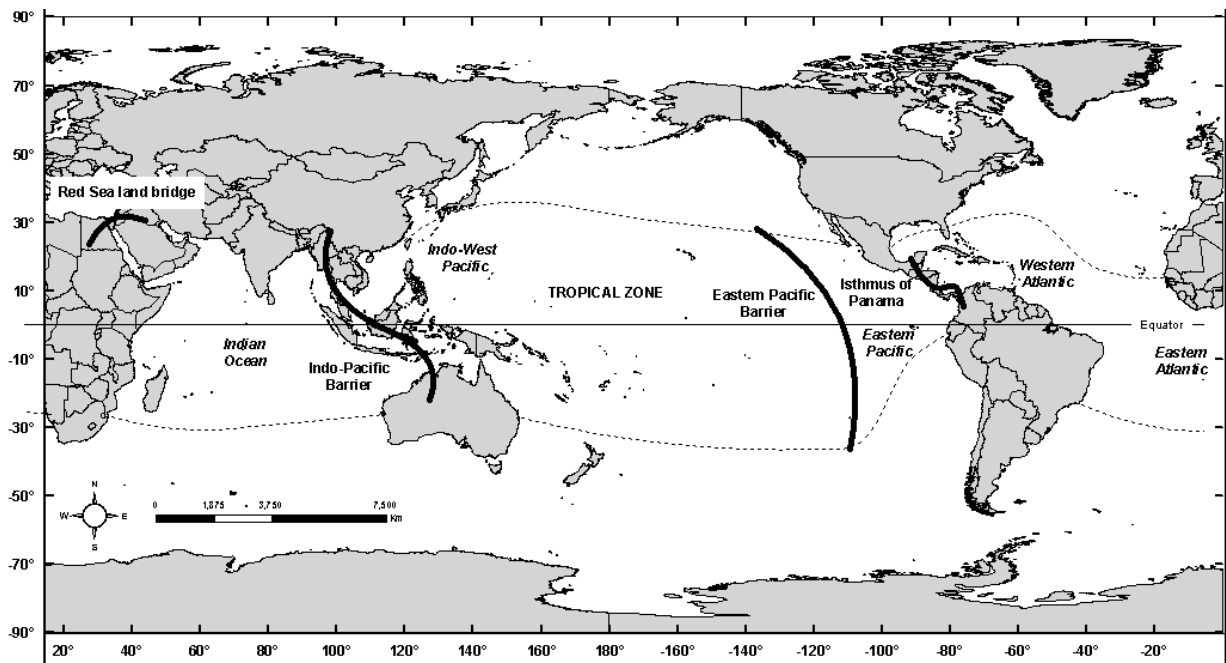
Fig. 1. Major physical factors affecting the global distribution of reef fishes, and resulting biogeographic regions.

Despite these divisions, there is broad taxonomic overlap of reef-associated fishes worldwide. Of the ten families that are considered to be characteristic of coral reef systems (Bellwood, 1996), few are restricted to only one region, and in most cases overlap is extensive at the genus level (Briggs, 1974). The Western Atlantic region, with 700 species of fish (Rocha, 2003), is essentially a more species-poor version of the tropical Pacific, which hosts more than 4000 fish species (Springer, 1982). The reef fish fauna of the Western Atlantic and the Eastern Pacific biogeographic regions are very similar, probably reflecting their connection prior to the closure of the Isthmus of Panama (Bellwood & Wainwright, 2002).

2.2 Historical barriers to dispersal

Over evolutionary history, geological processes have created a series of environmental barriers to dispersal that progressively separated reef fish taxa among the ocean basins. Cooling at high latitudes "locked in" the tropics 37 million years ago, restricting the movement of tropical species to a latitudinal band around the Equator now known as the Tropical Zone (Briggs, 2007). Later, the Atlantic and Indian oceans were cut off from each other when Africa collided with Eurasia 12-18 million years ago, and the uplift of the Isthmus of Panama around 5 million years ago separated the Atlantic from the Pacific. The last tropical connection between the ocean basins was effectively closed 2 million years ago by the formation of the Benguela upwelling, a cold-water barrier, off the Atlantic coast of southern Africa (Bellwood & Wainwright, 2002). These and other historical barriers to dispersal (Figure 1) prevented the exchange of individuals among populations, causing both extinctions and speciation events (Bellwood & Wainwright, 2002; Palumbi, 1994).

Biogeographic barriers that resulted in historical vicariance events can continue to hinder dispersal among populations. For instance, the Pacific has been divided into three major biogeographic regions: the Indian Ocean, the Indo-West Pacific, and the Eastern Pacific. The

barriers between these provinces include the world's largest uninterrupted expanse of deep ocean, the 4000 - 7000 km wide Eastern Pacific Barrier, which isolates the Eastern Pacific from the rest of the Pacific, and the Indo-Pacific Barrier, the dense mass of islands and continents (including Australia) that separates the Indian and Pacific Oceans (Figure 1). The latter barrier is enhanced during low sea level stands, when there are fewer passages between islands, and by strong upwelling that is likely to reduce the habitat available for tropical species (Barber et al., 2002).

2.3 How biogeography helps us to understand population connectivity

The present-day distribution of coral reef fishes is heavily influenced by physical and geological events in the history of the earth that defined the boundaries of the tropical region and the various ocean basins. In addition to the evolutionary-scale processes that have structured the distribution of tropical marine species, ecological processes act to maintain current distribution patterns (Bellwood & Wainwright, 2002). For instance, the scale of dispersal of reef fishes influence how populations within a species are spatially distributed (James et al., 2002). Due to the lack of visible obstructions in the marine realm and the presumed ability of larvae to passively disperse great distances, the prevailing paradigm for decades was that marine fish populations mixed freely and had high levels of connectivity throughout their ranges. In other words, the popular view was that marine populations were largely open, connected by demographically significant movement of individuals (immigration and emigration) (Hixon et al., 2002).

Biogeography tells us that species are not uniformly distributed throughout their ranges, and it is obvious that the long-held belief in freely dispersing marine populations discounts temporal and spatial variability in environmental conditions and dispersal patterns among sites. It became apparent only recently that barriers to dispersal, aside from delimiting distribution patterns in evolutionary time, could also structure populations of marine species on ecological time scales. The assumption of range-wide population openness has been challenged by a litany of recent studies showing that coral reef fish larvae, even of widely distributed species, often settle closer to their natal reefs than previously thought (Almany et al., 2007; Jones et al., 1999; Jones et al., 2005; Kingsford et al., 2002; Leis, 2002; Planes et al., 1998; Planes et al., 2001, Swearer et al., 1999; Taylor & Hellberg, 2003).

The nature of connectivity has important ecological and evolutionary implications. At one extreme, if reef fish populations are highly connected among patches, they may be more able to withstand local disturbances that degrade or remove habitat, and in the long term they may be less prone to local extinction. Under such open population models, we may expect only slow rates of evolution due to the very large effective population sizes. At the other extreme, if populations are isolated from one another, they may be more prone to local extinction as a result of habitat degradation or loss, since they are not supplemented by immigration of individuals from elsewhere. Further, over long periods of time genetic differences may build up such that reef fish populations become reproductively isolated, with the capacity to form new species.

The influence of connectivity on speciation is particularly relevant when discussing how historical context informs present-day population connectivity in reef fishes. Within the five major biogeographic regions of the tropics (the Indo-West Pacific, the Eastern Pacific, the Western Atlantic, the Eastern Atlantic, and the Indian Ocean), reef fish species are not evenly distributed. Rather, they have become concentrated into relatively small areas of

very high biodiversity. The Coral Triangle (also known as the East Indies Triangle) and the southern Caribbean are centers of diversity for the Indo-West Pacific and Western Atlantic regions, respectively. In the biogeographic provinces of the Coral Triangle and the southern Caribbean, at least 10% of the fauna are endemic species (Briggs, 1974). In the Coral Triangle in particular, speciation rates are so remarkable that Mora et al. (2003) observed that there seemed to be a continuous flow of species from the East Indies outward across the Indian and Pacific oceans.

Why are these particular areas of the tropics, specifically the Coral Triangle, effectively functioning as species factories? It is known that scales of dispersal influence speciation rates (Palumbi, 1994). Multiple, smaller scale barriers to gene flow clearly operate within the larger biogeographic regions, isolating populations by preventing dispersal among them. Barriers to dispersal that create population divisions within species on an ecological scale will become evolutionary-scale if they persist and lead to speciation or extinction. Biogeographical patterns of species distributions therefore simply reflect population structure that has been reinforced over evolutionary time. Indeed, studies are increasingly revealing that, even without obvious barriers to dispersal, populations of species that are morphologically alike are often divergent enough to be considered separate, or sibling, species (Knowlton, 1993).

The recognition that marine populations are not uniformly well mixed throughout their ranges has fundamentally changed the way biologists and ecologists think about the distribution of marine species, especially coral reef fishes. It is no longer enough to recognize habitat patchiness as a driver of population dynamics. We are now compelled to evaluate the scale of patchiness, or the relative openness, of each marine population in question, which may or may not correlate with the availability of suitable habitat. In other words, the question has become about the temporal and spatial scales of mixing among populations. Quantifying this connectivity is crucial for understanding local adaptation and speciation, population replenishment, and the likelihood of local extinction. While there are still examples of populations that appear to be highly open (Eble et al., 2011) as well as highly closed (Jones et al., 2005), the majority of reef fish populations likely lie somewhere along a continuum, and the important task going forward will be identifying where different organisms occur along this spectrum.

3. Quantifying connectivity by estimating larval dispersal

Despite its critical ecological importance, population connectivity remains notoriously difficult to quantify directly. Most coral reef fishes have a biphasic life cycle with a dispersive larval phase and a relatively less mobile adult phase. Movement from one site to another is thus accomplished mainly via larval dispersal, as opposed to adult migration. The pelagic stage of reef fishes is critical for connecting populations among patchy habitats but is arguably the least understood phase of their life cycle (Planes, 2002). In particular, the smallness of larvae relative to their vast and complex fluid environment (Mora & Sale, 2002) has hindered accurate quantification of dispersal and connectivity.

Both direct and indirect attempts have been made to measure larval dispersal. For decades, a popular method of tracking taxa such as whales (Ray et al., 1978) and tuna (Fink and Bayliff, 1970) has been tagging, in which a satellite or radio tag is physically attached to or implanted into the animal. These tags potentially yield a detailed record of movement over time. For obvious reasons, this approach is not possible with reef fish larvae, but another form of tagging has been attempted. A mark-recapture method has been developed that

involves tagging the otoliths of larval fishes by saturating the surrounding water with a chemical, such as tetracycline, that becomes incorporated into the calcium carbonate structure of the otolith (Jones et al., 2005; Thorrold et al., 2002). Later analyses of juvenile fish otoliths reveal the chemical signature. Such methods, however, are often prohibitively time-consuming and expensive, with low returns due to extensive larval mortality and dilution in the ocean. For instance, Jones et al. (1999) tagged over 10 million developing embryos of a damselfish (*Pomacentris amboinensis*) on the Great Barrier Reef in Australia. Of 5,000 juveniles subsequently settling at the same location, the authors retrieved 15 marked individuals (Jones et al., 1999), a return rate of just 0.00005%.

The many difficulties associated with direct tracking of larvae have encouraged the development of indirect, more efficient methods of estimating larval dispersal. Monitoring ocean currents is a relatively straightforward way to predict larval dispersal and adult migration (Cowen, 2002; Cowen et al., 2000; Lobel, 1997), but a major handicap of this approach is that it relies on the assumption that larvae drift passively with currents, which is not always true (Gerlach et al., 2007; Kingsford et al., 2002). In addition, long-term mean current patterns may differ from local or infrequent oceanographic conditions that could affect dispersal.

3.1 Genetics: From phylogeography to molecular ecology

It was first suggested in 1975 that genetic variation could be the best approach for assessing dispersal and migration among geographically separated populations of reef fishes (Ehrlich, 1975). In tandem with advances in the field of molecular ecology, in the past several decades the analysis of genetic information has emerged as a means to understand the distribution and diversity of marine species and populations (Bohonak, 1999; Burton, 1996, 2009; Grosberg and Cunningham, 2001; Hellberg et al., 2002; Shulman, 1998; Slatkin, 1987). This indirect method is possible because the dispersal of propagules maintains gene flow between geographically separated populations (Hellberg et al., 2002; Shanks et al., 2003). Genetics-based methods can infer gene flow, and therefore dispersal, through spatial variation in allele and genotype frequencies (Hedgecock et al., 2007; Planes, 2002). Therefore, the same factors that influence dispersal, or larval "flow", can be assumed to also influence gene flow (but see Section 3.2 for a discussion of caveats to this assumption).

On evolutionary time scales, the study of phylogeography assesses genetic diversity among species to examine historical processes that may be responsible for contemporary geographic distributions (Rocha et al., 2007). Phylogeographic approaches rely on genetic markers that reflect deep historical linkages among taxa in order to build gene genealogies, or trees, that help to explain contemporary species-level relationships. For instance, the Barcode of Life is a recent initiative to catalog diversity based on a region of the genome that varies in an easily identifiable, species-specific manner (Hebert et al., 2003).

Because biogeographic and ecological processes are linked, genetic information can also be used to evaluate whether connections exist among spatially segregated populations of the same species (Shulman & Bermingham, 1995); that is, are populations demographically open or closed (Mora & Sale, 2002) on ecological time scales? In theory, predictable recruitment and connectivity patterns are expected to drive stable genetic structure among populations (Purcell et al., 2006). If larvae are dispersed randomly and widely away from the parental populations, then no consistent genetic structure will occur. On the other hand, if larvae are returned to the parental population, then gene flow between geographically

separated populations will be restricted, and genetic structure will arise (Shulman & Bermingham, 1995).

Several well-known theoretical models of population genetic structure have existed since well before the application of genetic information to estimating larval dispersal. These models describe expected patterns of structure, given a certain set of conditions. For instance, the so-called isolation by distance pattern can arise in species with sufficiently large geographic ranges relative to their dispersal ability. Wright (1943) introduced this model to describe how genetic differences could accumulate over time, given restricted dispersal. In conjunction with the stepping-stone model of population structure (Kimura and Weiss, 1964), the isolation by distance model has developed to describe the population structure among organisms whose dispersal ability is constrained by distance, such that gene flow is most likely to occur between neighboring populations (Slatkin, 1993). Together, these approaches link gene flow with geographic distance (Planes and Fauvelot, 2002).

Predicting the population genetic structure that may result from a given pattern of larval dispersal, however, is not so straightforward, as there are many influences on dispersal besides geographic distance. It is important to explicitly consider all of the factors that influence dispersal, and therefore gene flow. Certain life history and behavioral traits, oceanographic conditions, and historical barriers to dispersal all influence whether geographically disjunct populations of coral reef fishes are connected via planktonic larval dispersal.

The variation in the magnitude of observed genetic structure may depend critically on the life history of the study species (Gerlach et al., 2007), such as the timing and location of spawning relative to currents, gyres, and tides (Pelc et al., 2009). Egg type and reproductive strategy also play a role (Leis & McCormick, 2002). The pattern of high gene flow for reef fish with a pelagic larval phase is supported by numerous examples of reef fishes that show no significant population structure over distances spanning thousands of kilometers (Craig et al., 2007; Horne et al., 2008; Klanten et al., 2007; Palumbi, 1994; Planes & Fauvelot, 2002; Riginos and Victor, 2001). Species with non-pelagic larvae such as clownfish and damselfish, meanwhile, tend to show strong genetic structure indicative of high levels of local recruitment (Jones et al., 1999). In a study of gene flow in eight reef fish species, Shulman & Bermingham (1995) found no evidence of genetic structure across the Caribbean except in species that lacked pelagic larvae.

The length of time that larvae spend in the water column has also been implicated as a factor affecting dispersal and genetic structure (Bowen et al., 2006; Weersing & Toonen, 2009). Reef fishes typically have larval lives lasting for weeks or months, seemingly long enough to achieve dispersal great distances away from the source population. It seems intuitive that the longer a larval propagule stays in the water column, the farther it will travel. However, there is no consistent correlation between pelagic larval duration (PLD) and geographic range size (Lester et al., 2007; Lester & Ruttenberg, 2005; Victor & Wellington, 2000), or between PLD and population genetic structure (Weersing & Toonen, 2009). Previously reported correlations appear to have been driven by species lacking a pelagic larval phase (Eble et al., 2011). Reproductive strategy may thus be a stronger influence than PLD on dispersal. Larvae can also actively participate in their own dispersal through evolved behaviors such as "smelling home" (Gerlach et al., 2007) and navigating toward sensed targets, which in sum can promote local retention.

Superimposed on the patterns of variable life history traits is the larger pattern of abiotic influences on dispersal, including oceanographic features such as currents, eddies, tides,

and fronts (Cowen, 2002). It is well known that larvae of marine species can accumulate at fronts (Roughgarden et al., 1991). Regional currents, as well as secondary or indirect currents, are also important (Visram et al., 2010). As our understanding of ocean physics improves, the role of advection and diffusion in larval dispersal is also beginning to be appreciated (Largier, 2003). Points, jets, and retention zones can cause variable larval transport along coastlines (Gaylord and Gaines, 2000; Largier, 2004; Richards et al., 1995). Seasonal shifts in current patterns and episodic events such as relaxation of upwelling (Largier, 2004) may have significant consequences for larval transport and recruitment. At large scales (greater than 300 km), studies have linked areas of strong genetic structure in fishes and corals to major oceanographic and environmental features (Baums et al., 2006; Galarza et al., 2009; Galindo et al., 2006; Pelc et al., 2009).

Finally, studies have shown that even marine species with high dispersal potential break into genetically similar groups within biogeographic provinces (soldierfish, Craig et al., 2007; surgeonfish, Planes and Fauvelot, 2002). For instance, Barber et al. (2000) observed a sharp, localized genetic break among stomatopod populations in Indonesia, suggesting a marine counterpart to the Wallace's line that separates terrestrial fauna there. These results demonstrate that biogeographic provinces that were formed millions of years ago can still function as barriers to dispersal today, even in widely ranging species (Barber et al., 2000).

3.2 The double-edged sword of molecular ecology

Predicting patterns of genetic structure is inherently difficult, and empirical measurements often fail to correspond to predictions. In the Pacific, biogeographic divisions do not appear to affect the dispersal of some reef fish species, possibly due to the extensive mixing and unstable circulation generated by El Niño events and other phenomena (Muss et al., 2001). Limited genetic subdivision across reefs of the Pacific has been demonstrated in a number of reef fishes, such as surgeonfish (DiBattista et al., 2011; Eble et al., 2011; Horne et al. 2008; Klanten et al., 2007), grouper (Rivera et al., 2011), parrotfish (Bay et al., 2003), snapper (Evans et al., 2010), and angelfish (Schultz et al., 2007). Some species have been shown to traverse even biogeographic barriers that were thought to be insurmountable, such as the Eastern Pacific Barrier (Lessios & Robertson, 2006; Figure 1). Conversely, sometimes population genetic structure is observed despite an apparent lack of barriers to dispersal (Planes et al., 1998; Taylor and Hellberg, 2003; Toonen et al., 2011).

These discrepancies have several possible explanations related to the power of genetic analyses to resolve ecologically meaningful patterns. If genetic structure is present, but weak, then deciding whether populations are open or closed at the scale in question can be difficult (Hepburn et al., 2009). Moreover, though some of the factors producing population genetic structure are intimately related to demographic processes, others are not. Though it is commonly assumed that genetic structure reflects a balance between gene flow and genetic drift, migration and dispersal are not the only influences on genetic differentiation. Other forces such as natural selection and historical contact between populations can influence the allele frequencies used to evaluate levels of dispersal (Bohonak, 1999; Planes, 2002). For instance, even if gene flow is occurring, natural selection can be a major force maintaining genetic differentiation among populations (Mora & Sale, 2002). Patterns over evolutionary time (natural selection and historical contact) can therefore influence the genetic structure observed in ecological time, and this is cause for caution when interpreting

genetic data as a reflection of demographic patterns. Furthermore, because an exchange of just one individual per generation can result in genetic homogeneity (Planes, 2002), populations may be linked genetically without an obvious demographic connection (Kool et al., 2010). When interpreting genetic patterns in the context of ecology, then, it is critical to discriminate based on temporal scale, delineating evolutionary versus ecological connectivity.

Adding complexity to studies of connectivity is selecting genetic markers, a process that is rife with controversy even within the molecular ecology community (Fauvelot et al., 2007; Hellberg, 2007, 2009). Because different markers have different spatial and temporal powers of resolution, great care must be taken in both selecting markers and interpreting patterns of genetic structure obtained from analyses of variation in those markers. Two types of markers that are commonly used in genetic studies, allozymes and mitochondrial DNA (mtDNA), are not very sensitive to genetic drift at the appropriately short temporal scales (Hellberg, 2009). These types of markers are useful for evaluating the evolutionary relationships of closely related populations and for inferring connectivity over longer temporal scales. Demographic studies, on the other hand, require that markers are able to drift distinctively among populations at temporal scales that are relevant to population replenishment. For these types of studies, other DNA markers called microsatellites are promising alternatives to the more traditionally used allozymes and mtDNA. Microsatellites are gaining popularity among molecular ecologists because they have a high mutation rate and are probably neutral to selection (Hellberg, 2009). Their mutation rate is high enough to result in a large amount of variation among unrelated individuals within a population, but low enough so that changes usually do not occur more often than every few generations (Hartwell et al., 2008). Microsatellites can therefore detect subtle differentiation among closely related individuals, which is useful for determining ecologically relevant connectivity as opposed to more historical population subdivisions (Hellberg, 2009). Ideally, to begin to address these differences, population connectivity studies should at least compare results obtained from multiple markers.

Finally, different methods of characterizing genetic structure and estimating gene flow make different assumptions about the equilibrium status of populations, migration patterns, population structure, and the attributes of genetic markers (Grosberg & Cunningham, 2001). Sampling protocols are widely variable, as are geographic and temporal scales surveyed. In addition to the inherent limitations of using population genetic structure to infer dispersal, this lack of a cohesive approach further complicates the interpretation of genetic structure analyses.

There are several ways to counteract the pitfalls inherent in a molecular ecology approach. More direct genetic methods for tracking larvae, such as parentage analysis (Christie et al., 2010; Jones et al., 2005; Planes et al., 2009; Saenz-Agudelo et al., 2009), are gaining traction, but this approach is really only feasible with strongly site-attached taxa such as clownfish, where brooded larvae can be easily associated with a parental source. Other recent genetic advances include the ability to resolve the high temporal variation in reproduction and recruitment patterns that commonly occurs among Caribbean and Pacific reef fishes (Sale et al., 2005). At small scales, this temporal variation produces a complex pattern called chaotic genetic patchiness (Johnson & Black, 1982), which remained unexplained until recently (Selkoe et al., 2010). It is important to detect the causes of this variability, as spatial and temporal variation in connectivity may itself help to promote long-term stability in populations (Hogan et al., 2010).

3.3 Integrating multiple types of data: An example from the Caribbean

There is a growing recognition that, given the complexity of larval dispersal, genetic data are most useful when analyzed in tandem with models, oceanographic data, or other approaches (Galindo et al., 2006; Rivera et al., 2011; Selkoe et al., 2008). In the absence of inexpensive, effective methods of directly measuring larval dispersal, such integrated approaches represent the next best strategy to obtain ecologically meaningful data, as emphasized in the following example from the Caribbean.

The Caribbean is an essentially closed ocean basin with relatively stable current systems since the shoaling of the Isthmus of Panama around three million years ago (Briggs, 2007). The basin is biogeographically isolated from the southwestern tropical Atlantic (e.g., Brazil) by the inter-regional barrier of the Amazon outflow, and from the eastern tropical Atlantic (e.g., western Africa) by sheer distance (Floeter et al., 2008). Within the Caribbean, species distribution patterns suggest that there are few biogeographic divides for reef fish, with most species ranges spanning the entire basin. As such, species richness across Caribbean islands is predicted best by island size and distance from neighbors, rather than by taxon-specific dispersal histories (Sandin et al., 2008). The biogeography and oceanography of the Caribbean would seem to indicate a strong potential for population connectivity, and therefore genetic similarity, across the basin. Given its stepping-stone geography and a total distance along a current track of 4500 km, Shulman & Bermingham (1995) suggested that it could take as few as 13 generations for a novel haplotype to spread throughout the basin. Correspondingly, studies have shown high rates of gene flow in reef fish leading to genetic similarity within taxa throughout the Caribbean (Lacson, 1992; Shulman & Bermingham, 1995).

In contrast, a model by Kool et al. (2010) showed that, while reef fish populations in the Caribbean became increasingly genetically connected with one another over time, relative differences between populations persisted, providing the basis for the development of genetic structure. Similarly, a biophysical model by Cowen et al. (2006) identified four broadly defined, distinct regions of population isolation: the eastern Caribbean, the western Caribbean, the Bahamas-Turks and Caicos Islands, and the region at the periphery of the Panama-Colombia gyre. These regions correspond to genetic and morphological clines observed across a range of marine organisms (Cowen et al., 2006). Given the significant degree of structure expected to be present in the Caribbean from these model simulations (Cowen et al., 2006; Kool et al., 2010), why are strong breaks between populations not more evident in observations of natural populations (Purcell et al., 2006; Shulman & Bermingham, 1995)? This discrepancy may occur because sampling a limited number of individuals decreases the amount of visible structure (Kool et al., 2010). That empirical studies may be inherently limited by sampling power relative to model simulations is therefore an important consideration in evaluating results of population genetic studies.

4. How do we account for this variability? A model of passive and active dispersal

When considering the pronounced variation in the biotic and abiotic factors determining dispersal, it is unsurprising that published estimates of connectivity and dispersal in coral reef fishes vary widely (Cowen et al., 2006; Purcell et al., 2006; Gerlach et al., 2007; Hepburn et al., 2009) and that no general relationship between spatial scale and the likelihood of population-level genetic divergence has emerged (Hepburn et al., 2009). Given the complexities and simplifying assumptions involved in equating gene flow with dispersal, this variability is

partly a relic of the genetics methods used to estimate dispersal. The majority of marine species have high rates of gene flow over evolutionary time scales (Hedgecock et al., 2007). Determining the extent to which populations are connected on an ecological scale, despite high gene flow at an evolutionary scale, remains the single greatest challenge for revealing ecologically meaningful patterns of larval dispersal (Botsford et al., 2009).

The case study from the Caribbean illustrates this dichotomy between evolutionary gene flow and ecologically relevant dispersal. Even though studies have shown genetic similarity across the Caribbean, suggesting basin-scale mixing among reef fish populations (Geertjes et al., 2004; Lacson, 1992; Shulman & Bermingham, 1995), the ecologically meaningful pattern of larval dispersal is likely at the regional scale (Cowen et al., 2006). Isolation in reef fish populations at this scale has also been shown in other oceanographically and geographically complex regions such as the Indo-Pacific (Drew et al., 2008).

The paradigm shift in marine population connectivity means that, on ecological time scales, reef fish populations are now considered to be substantially closed, rather than broadly open (Mora & Sale, 2002). Effective dispersal is much smaller than potential dispersal extrapolated from ocean current speed and pelagic larval duration (Planes, 2002). We may therefore expect a relatively narrow dispersal kernel for most species, with most offspring settling near to the location where they were produced (Figure 2). This pattern of enhanced local retention (Roberts, 1997) can be explained by active, as opposed to passive, mechanisms limiting the distances that most offspring disperse. Reef fish can employ a suite of spatial, temporal, and behavioral adaptations that interact with local oceanographic conditions to enhance local retention of larvae (Kingsford et al., 2002; Sponaugle et al., 2002; Figure 2).

In the passive model, larval density is best approximated as a normal distribution generated by a random-walk model of movement away from natal reef. Local retention of larvae is fairly evenly balanced with widespread dispersal. This pattern is produced if adult fishes do not spawn preferentially near ocean currents that would keep larvae close to shore, if spawning occurs regardless of lunar phase, and if larvae drift passively with ocean currents once spawned. In the active model, however, local retention of larvae is enhanced, and widespread dispersal is substantially reduced (to about 10% of offspring). This pattern can arise from spawning aggregations near ocean currents that retain larvae near the coast (Lobel, 1989), from spawning timed to a particular lunar phase, and from active swimming behaviors of larvae that allow them to respond to stimuli from their natal reef (Gerlach et al., 2007). It can be difficult to resolve the spatial and temporal scales at which each factor is most important, but this is critical to understanding marine population connectivity, since the interaction of life history and oceanography produces an emergent pattern that is not obvious with empirical genetics work alone (Cowen et al., 2006; Kool et al., 2010).

Dispersal in general is important in selecting habitat, finding unoccupied sites to settle, escaping locally deteriorating environments, founding new populations, and bet hedging on the part of the parental population (Strathmann et al., 2002). However, none of these objectives requires long-distance dispersal, and many actually can be accomplished more successfully by dispersing shorter distances. For instance, long-distance dispersers do not make the best colonizers of new habitat. They may be able to reach new areas more often than shorter distance dispersers, but once they arrive, their highly dispersive larvae will simply be exported from the site (Strathmann et al., 2002). Marine populations therefore achieve closure by developing life histories that retain offspring as members of the reproductive unit (Strathmann et al., 2002).
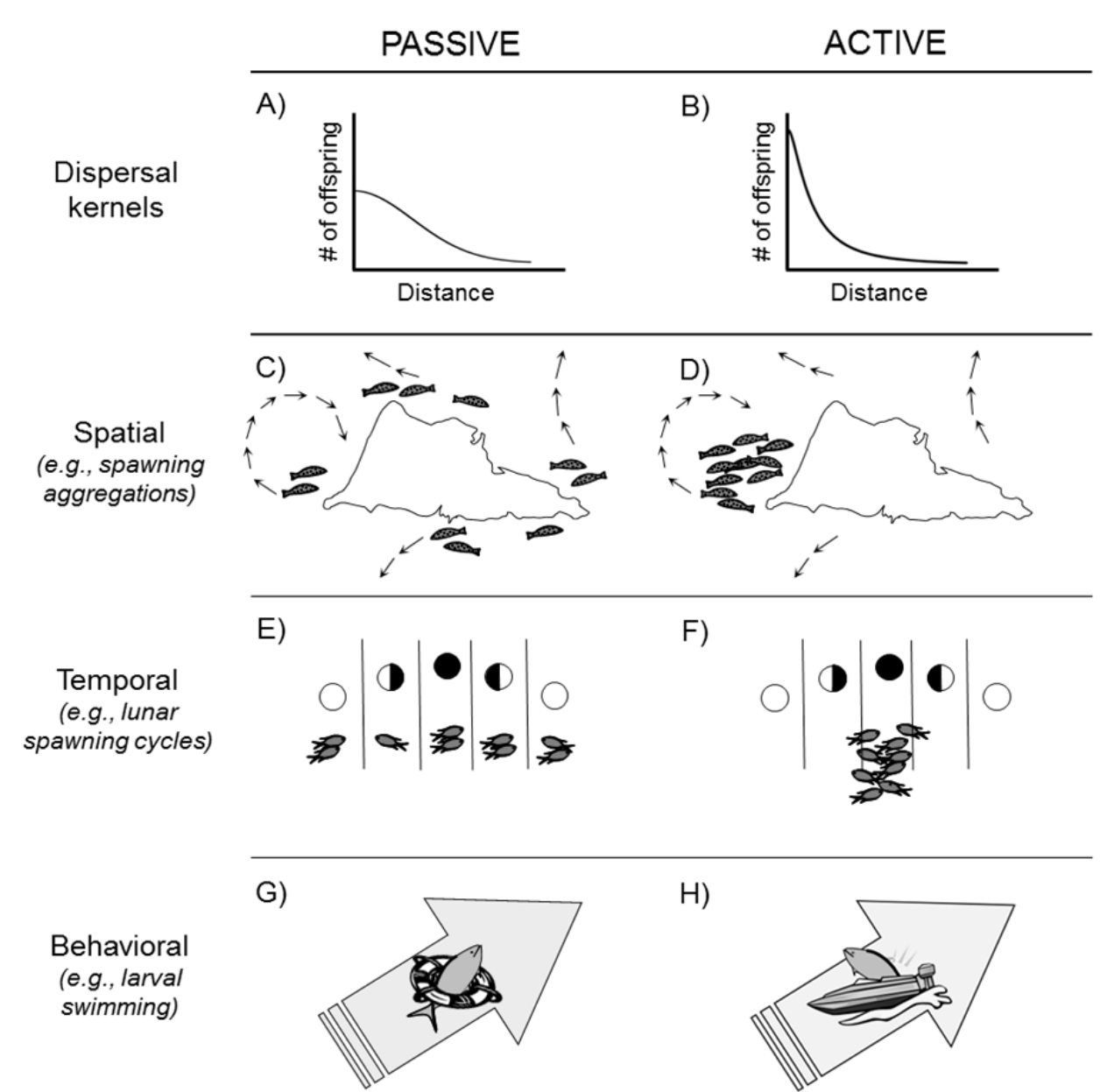
Fig. 2. Passive versus active models of dispersal in coral reef fish. (A & B) Dispersal kernels describing the density of offspring with increasing distance from a natal reef. Active processes tend to increase the density of offspring near to the source reef (as noted by leptokurtic distribution). A number of species-specific mechanisms can generate limited dispersal. (C & D) Spawning fish can aggregate in areas near favorable ocean currents, for example retention eddies. (E & F) Adult fish can time spawning during times of slack tides, reducing advection of larvae from natal reefs. (G & H) Larval fish can employ active behaviors (e.g., ballooning across depth strata or swimming) to maintain position near to natal reefs.

If local retention of larvae is so important, why then do about 10% of reef fish larvae disperse far from home? A traditional explanation of widespread dispersal suggests that it

could result from the relatively long larval life of many reef fishes, stepping-stone dispersal, travel by larvae in major currents and coastal countercurrents, and/or changes in the direction of major currents over time scales of hundreds to thousands of years (Shulman & Bermingham, 1995). In contrast, widespread dispersal in reef fishes could also simply be a byproduct of selective pressures that actually favor dispersal over shorter distances, closer to the parental population (Strathmann et al., 2002). For instance, the pelagic phase could have itself developed as an ontogenetic migration into the water column so that larvae can avoid demersal predators, access richer food resources, and/or escape parasites (Johannes, 1978; Swearer et al., 2002). The relatively small percentage of widely dispersing larvae therefore represents "the ones that got away", perhaps carried off by ocean currents. Widely dispersing larvae therefore comprise the tail of a dispersal distribution centered around the parent population. Wide dispersal could also represent an intentional temporary migration away that is followed by a return back to the source area. In other words, larvae that are transported away from their parents will not necessarily settle away from their parents (Strathmann et al., 2002). Even if initially transported several hundred kilometers away, the majority of larvae will recruit close to home (Planes, 2002; Strathmann et al., 2002).

As discussed in earlier sections, genetic similarity between populations can be reinforced by as few as one migrant (or larval propagule) per generation (Planes, 2002). The very existence of long-distance dispersal therefore has genetic consequences, perhaps leading to homogeneity over a large area. However, this model of dispersal posits that demographic (and therefore, ecologically relevant) consequences are driven primarily by patterns of local dispersal and subsequent recruitment (Strathmann et al., 2002).

4.1 What defines "home"?

Though the 90% close to home/10% far away model of reef fish larval dispersal may be generally true, the geographic distance defining "close to home" depends on the interaction between life history and oceanography, which in turn depends on location and taxa. For instance, even in the absence of any apparent barriers, some Pacific reef fishes with a high dispersal capacity demonstrate high genetic divergence among populations (Fauvelot & Planes, 2002; Planes et al. 1996; Planes & Fauvelot, 2002; Riginos and Victor, 2001). This may be related to the degree of isolation of Pacific islands, which makes them good candidates for studies of elevated self-recruitment and other dispersal patterns (Planes et al., 1996; Treml et al., 2008). Because Pacific islands are so far away from each other relative to Caribbean islands, it is logical to expect that local (within-island) retention on ecological scales is more important in the Pacific than in the Caribbean, since longer distance dispersal is unlikely to be sufficiently great to allow larvae to settle at a very distant island. In other words, "close to home" for a reef fish in the Pacific may be at the within-island or within-reef scale, where "close to home" in the Caribbean may be among several relatively closely spaced islands or reef habitats. In addition, the definition of "close to home" is also variable among taxa. Because damselfish and clownfish are brooders, their "close to home" is their coral territory or anemone, respectively. What qualifies as "home" is likely to cover a wider area for species that spawn into the water column. Furthermore, life history traits such as egg size, larvae size, pelagic larval duration, and larval growth rates can vary within reef fish families among different ocean basins (Thresher and Brothers, 1989), supporting the idea that life history traits related to reproduction have evolved to optimize local oceanographic conditions.

5. Connectivity is relevant to the management and conservation of coral reef ecosystems

Coral reefs, which have been called the rainforests of the sea (Connell, 1978), are some of the most biodiverse and productive ecosystems on the planet. They contain an estimated 25% of all marine species, including thousands of species of fish. Millions of marine species live primarily or exclusively in association with coral reefs. In addition, the economic, social, and cultural importance of coral reefs to humans cannot be overestimated. Over 1 billion people worldwide depend directly on reef resources such as fish, creating an intimate link between reef ecosystem functionality and human wellbeing.

Despite their immense biological and ecological significance, as well as their demonstrated importance to humans, coral reefs are one of the most highly impacted ecosystems on the planet (Halpern et al., 2008). Stressors such as climate change, overfishing, and pollution are causing distributional shifts and biodiversity loss in coral reef ecosystems in many regions of the world (Birkeland, 2004; Graham et al., 2006, 2007; Hughes et al., 2003; Jones et al., 2004; Munday, 2004; Munday et al., 2008; Pandolfi et al., 2003; Wilson et al., 2006, 2008, 2009). In the face of these numerous threats, an improved knowledge of evolutionary and ecological patterns of reef fish connectivity is needed in order to design effective marine protected areas that both conserve biodiversity and enhance fisheries (Almany et al., 2007, 2009; Jones et al., 2009; Palumbi, 2003; Russ, 2002; Sale et al., 2005). In addition, identifying ecological connectivity patterns between fragmented populations can indicate the resilience of species and ecosystems to changing environmental conditions (Jones et al., 2009, 2010; McCook et al., 2009; Planes et al., 1996; Steneck et al., 2009). For instance, because dispersal sustains populations with new recruits (Shanks et al., 2003), high connectivity can both buffer populations from local extirpation and, in the event of a population decline, facilitate post-disturbance recovery.

6. Conclusions and directions for future research

Reef fish populations are heterogeneously distributed in space and time, reflecting both the evolutionary origins and ecological maintenance of distribution patterns. Biogeography can be used to inform contemporary patterns of distribution and dispersal. The recognition that reef fish populations could experience high levels of local recruitment and limited larval dispersal was an important paradigmatic shift that refocused studies onto understanding the degree of connectivity among populations, which has important ecological and evolutionary implications. The fact that reef fish dispersal occurs primarily via larval propagules, however, means that connectivity has resisted easy quantification. In order to achieve a more complete picture of population connectivity patterns among coral reef fishes, it must be a research priority to better understand the spatial and temporal variability in larval dispersal and recruitment dynamics across taxa, as well as across ocean basins. This will necessarily involve the development of more sophisticated biophysical models that should be used in conjunction with empirical approaches. Methods that relate genetic structure to estimates of dispersal have been useful, but due to their limitations, they represent only a fraction of the suite of tools that will be necessary for resolving demographically relevant connectivity patterns in reef fishes. A generalized model of dispersal distance based on our current understanding of these patterns proposes that the majority of larvae stay close to home rather than dispersing widely.

Future research should also bear in mind the influence of anthropogenic factors on connectivity patterns in marine populations. Climate change-related increases in ocean temperatures and changes in weather patterns are projected to alter the speed and direction of major currents, which will affect the physical transport of larvae (Cowen & Sponaugle, 2009). In addition, increasing habitat fragmentation may play a role in the widely reported local-scale genetic structure in coral reef fishes (Salas et al., 2010), and the benefits of local retention and larval transport are likely to erode in degraded environments (Jones et al., 2009). The disruption of natural patterns of larval retention and connectivity has thus been proposed as a key factor threatening reef fish populations in the coming century (Jones et al., 2009). Given the vulnerability of coral reef ecosystems to global change and other stressors, a more explicit understanding of population connectivity patterns in reef fishes is crucial to their effective management and conservation.

7. Acknowledgements

8. References

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Changing Diversity in Changing Environment

Edited by PhD. Oscar Grillo

As everybody knows, the dynamic interactions between biotic and abiotic factors, as well as the anthropic ones, considerably affect global climate changes and consequently biology, ecology and distribution of life forms of our planet. These important natural events affect all ecosystems, causing important changes on biodiversity. Systematic and phylogenetic studies, biogeographic distribution analysis and evaluations of diversity richness are focal topics of this book written by international experts, some even considering economical effects and future perspectives on the managing and conservation plans.

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