

# Phylogeography and the conservation of coral reef fishes

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**Abstract** Here we present a review of how the study of the geographic distribution of genetic lineages (phylogeography) has helped identify management units, evolutionary significant units, cryptic species, and areas of endemism, and how this information can help efforts to achieve effective conservation of coral reefs. These studies have confirmed the major biogeographic barriers that were originally identified by tropical species distributions. Ancient separations, identified primarily with mtDNA sequence comparisons, became apparent between populations on each side of the barriers. The general lack of correlation between pelagic larval duration and genetic connectivity across barriers indicates that life history and ecology can be as influential as oceanography and geography in shaping evolutionary partitions within ocean basins. Hence, conservation strategies require a recognition of ecological hot-spots, those areas where habitat heterogeneity promotes speciation, in addition to more traditional approaches based on biogeography. Finally, the emerging field of genomics will add a new dimension to phylogeography, allowing the study of genes that are pertinent to recent and ongoing differentiation, and ultimately providing higher resolution to detect evolutionary significant units that have diverged in an ecological time scale.

**Keywords** Biogeography · Genetics · Connectivity · Phylogeny · Gene flow · Marine fish

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## Introduction

The field that addresses the geographical distribution of genetic lineages within species and investigates factors that shaped their genetic architecture is collectively known as phylogeography. Research in this field is capable of identifying previously unrecognized units of biodiversity, areas rich in unique populations and management units, and can yield insights into processes affecting the formation of new species (reviewed in [Avice 2000](#)). Recent advances in genetic techniques have increased the relative ease with which data may be generated and have facilitated the development of complex analytical approaches by which we may investigate population processes at time scales ranging from ecological to evolutionary.

Phylogeographic studies now include genetic assays of several marine species. Studies that survey multiple species across the same general area (comparative phylogeography) often identify congruent patterns of genetic lineage distributions and may indicate where areas containing evolutionarily significant units (historically isolated sets of populations, [Moritz 1994](#)) are located, thus providing guidelines for conservation priorities ([Moritz and Faith 1998](#)). While this approach has worked very well in terrestrial habitats, some aspects of life history parameters in marine species can confound genetic surveys. Notably, most coral reef organisms disperse by means of a pelagic larval stage and are relatively sedentary during the longer benthic and reef associated life stage ([Leis 2002](#); [Mora and Sale 2002](#)). The presence of this pelagic larval stage potentially increases gene flow among distant locations and overwhelms genetic divergence. However, recent advances indicate that active behaviour of larvae, local oceanographic processes and spawning events that coincide with certain tides and current regimes are among the biological

and physical factors that may influence larval dispersal by increasing local retention (Cowen 2002; Cowen et al. 2006). Consequently, the previously accepted view of largely open populations of coral reef organisms is shifting towards a realization that some species have several genetically interconnected, but demographically discrete populations (Leis 2002; Swearer et al. 2002).

The need for a better understanding of dispersal in the sea is urgent, mainly because the overall health of coral reefs has been on the decline worldwide, with over-exploitation, pollution, disease and climate change among the top threats to this unique tropical ecosystem (Pandolfi et al. 2003; Bellwood et al. 2004). Marine protected areas have been the primary means to protect coral reefs, and with the growing number of such areas (Mora et al. 2006), the questions of where to place reserves and how they should be spaced are becoming increasingly urgent (Halpern et al. 2006). To answer these questions researchers must: (1) assess local biodiversity to identify areas where protection would shelter the largest number of species, including unique lineages with a restricted geographical range (Moritz and Faith 1998); and (2) estimate dispersal of the organisms in order to design reserve networks that would promote both effective species protection and spill-over to non-protected areas (Palumbi 2004).

Phylogeography assumes a central role in assessing these questions by analysing the genetic relationships between distant populations that may be separated by vast expanses of unsuitable habitat (open ocean, sand bottoms, etc.) but connected to varying degrees by larvae carried by oceanic currents. If distant populations have strong genetic ties, high dispersal ability is assumed (Rocha et al. 2002; Klanten et al. 2007); however, if they are genetically distinct, then limited dispersal, geographic barriers, or ecological factors can be involved in shaping the species evolution (Munday et al. 2004; Rocha et al. 2005a; Faucci et al. 2007).

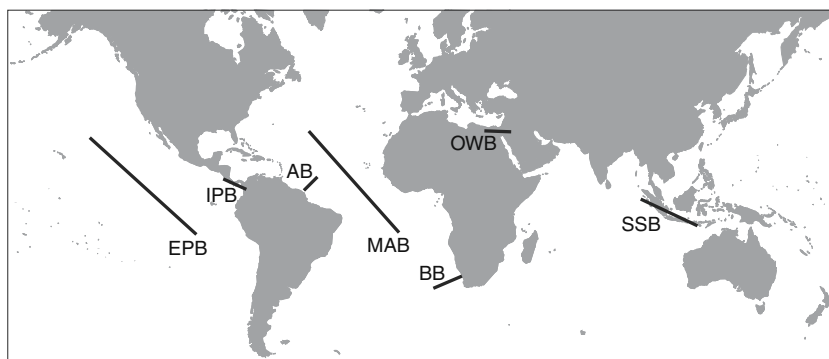
Thus, results from phylogeography studies can be applied not only to questions of evolutionary significance, but also have management applications. Hellberg (2007) has reviewed the impacts of phylogeography on ecological

time scale connectivity studies and provided valuable advice for future research directions. Here we concentrate on historical evolutionary processes detected mainly through phylogeographic surveys of fishes, but examples from other marine organisms (we limit the examples on corals, reviewed by van Oppen and Gates 2006) are used to illustrate marine phylogeographic patterns and to show how they relate to reef conservation and biogeography.

### Biogeographic barriers

Marine biogeographic barriers have been recognized for decades, and early researchers used breaks in the faunal composition and levels of endemism to designate geographic units or “faunal provinces”. In tropical marine habitats, only a few barriers are apparent and well studied (Fig. 1): (1) the junction between Africa and the Middle East, separating the Mediterranean from the Indian Ocean is the Old World barrier, formed after the closure of the Tethys sea (reviewed in Ekman 1953; Briggs 1974); (2) the Caribbean Sea and the tropical eastern Pacific are separated by the New World barrier, formed after the closure of the Isthmus of Panama (reviewed in Bermingham et al. 1997; Knowlton and Weigt 1998); (3) the immense freshwater and sediment outflow of the Amazon river in north-eastern South America separates Brazil from the Caribbean and is known as the Amazon barrier (reviewed in Rocha 2003); (4) the cold water upwelling around southern Africa separates the tropical Atlantic from the Indian Ocean and is known as the Benguela barrier (reviewed in Rocha et al. 2005b); (5) the shallow continental shelf (Sunda shelf) among Indonesian islands is exposed during low sea levels, forming a long land bridge and restricting exchange between the tropical Indian Ocean and the western Pacific (reviewed in Randall 1998); (6) the vast open ocean distances between the tropical eastern Pacific and the islands of the central Pacific form the East Pacific barrier (reviewed in Lessios and Robertson 2006); and (7) the mid-Atlantic barrier consists of the open ocean distances separating the Americas and Africa (reviewed in Muss et al. 2001).

**Fig. 1** Geographic location of the seven major tropical marine biogeographical barriers. *EPB* Eastern Pacific Barrier, *IPB* Isthmus of Panama Barrier, *AB* Amazon Barrier, *MAB* Mid-Atlantic Barrier, *BB* Benguela Barrier, *OWB* Old World Barrier, *SSB* Sunda Shelf Barrier



In addition, several minor barriers have been identified. In the Caribbean, the Mona Passage separates the fauna in the Lesser and Greater Antilles (Hastings and Springer 1994; Baums et al. 2006; Taylor and Hellberg 2006); in the south-eastern United States, a strong temperature gradient along the Florida peninsula separates Atlantic and Gulf of Mexico populations (Avisé 2000); in the South Atlantic, opposite current directions and divergent ecological conditions separate populations north and south of the “hump” of Brazil (Santos et al. 2006); in the tropical eastern Pacific, long stretches of sandy coast and different temperature regimes separate three faunal provinces (Panamic, Mexican, and Cortez; Hastings 2000), with finer divisions within the Sea of Cortez (Riginos 2005); in the warm temperate eastern Pacific, circulation changes along Point Conception are apparently responsible for large faunal breaks (Burton 1998 and references therein); in South Africa the coastline is divided into three regions characterized by large variations in hydrological conditions (Teske et al. 2006 and references therein).

Even though these barriers represent significant faunal breaks, there is a large overlap in species composition between adjacent biogeographic provinces. For example, Brazil and the Caribbean share approximately 75% of their species (Rocha 2003). This is where phylogeography comes into play to help management decisions: should populations on both sides of these barriers be treated as distinct management units? Recent phylogeographic surveys indicate that the answer in most cases is yes. In the Atlantic, populations of the surgeonfish *Acanthurus coeruleus* and the wrasse *Halichoeres bivittatus* are significantly different between Brazil and the Caribbean (Rocha et al. 2002, 2005a). In the eastern Pacific, populations of many fish species surveyed in the Gulf of California are significantly different from those in the adjacent Pacific waters (Bernardi et al. 2003; Bernardi and Lape 2005). In the Indo-Pacific, bullethead parrotfish (*Chlorurus sordidus*) and three-spot seahorses (*Hippocampus trimaculatus*) show significant population structure among locations separated by the Sunda shelf barrier (Bay et al. 2004; Lourie and Vincent 2004a).

The level of genetic divergence among those faunal provinces varies extensively, from population (shifts in allele frequency) to species level separations (herein defined as separations supported by independent lines of evidence, or by genealogical concordance, sensu Avisé and Ball 1990). This prompts a recurring question: is the duration of the pelagic larval stage, often regarded as an indicator of dispersal potential, related to population structure? Several recent surveys indicate no relationship. In a survey of 15 Atlantic reef fishes, Bowen et al. (2006b) found no link between the larval duration and genetic divergence. In the tropical eastern Pacific, no correlation was detected

between larval duration and the geographical range of 44 species of wrasses and damselfishes (Victor and Wellington 2000). Often, the species biology and ecology (i.e. how the species interacts with the barrier), larval behaviour, and environmental differences were considered more important than larval duration per se (Shulman and Bermingham 1995; Riginos and Victor 2001; Rocha et al. 2005a; Bay et al. 2006; Choat 2006). However, cowries (gastropod family Cypraeidae) represent a notable exception: when Paulay and Meyer (2006) eliminated confounding factors such as dispersal estimation error, intraspecific variation and phylogenetic bias, they observed a significant positive correlation between the length of the pelagic larval stage and species ranges.

Comparative studies of closely related species can be especially informative because, as in the cowrie study indicates, these can eliminate confounding factors linked to deep evolutionary separations. The phylogeography of three sympatric Atlantic surgeonfishes in the genus *Acanthurus* with almost identical pelagic larval duration was strongly correlated to their adult habitat preferences and not to dispersal ability (Rocha et al. 2002). Similarly, five wrasses of the genus *Halichoeres* belonging to a monophyletic group (Barber and Bellwood 2005), with the same pelagic larval duration and overlapping western Atlantic distributions, showed genetic divergences that varied from 0 to species level separations across the Amazon barrier (Rocha 2004; Rocha et al. 2005a). Thus, larval dispersal ability may be strongly correlated to geographic ranges and genetic structure in species that have extreme (very long or very short) pelagic larval stages (Bay et al. 2006; Purcell et al. 2006), but it remains a poor predictor of population structure for coral reef organisms with the common pelagic larval durations between 3 and 5 weeks (Bowen et al. 2006b).

Phylogeography studies are often aimed at addressing large-scale evolutionary patterns related to strong biogeographic barriers; yet frequently recover patterns of relationships within species that have direct implications for management. One example is the realization that the placement of genetic breaks, especially in those species that have limited dispersal, corresponds not only to the major biogeographical barriers listed above, but also to previously unrecognized zones of environmental transition. Earlier work indicated that sharp genetic breaks within a putative species often corresponded to shifts in faunal assemblages (Avisé 1992). However, a study of intertidal copepods (genus *Tigriopus*) along the coast of California determined that the presence of a sharp genetic break coincident with the primary biogeographic partition in the area (Point Conception) was no deeper than five other genetic breaks found throughout the species range (Burton 1998). Similarly, sharp genetic breaks in mantis shrimp (genus *Haptosquilla*) coincident

with the Sunda shelf barrier in Indonesia were no deeper than breaks between Sulawesi and Papua or even between two locations along the coast of Papua, where no biogeographic break is recognized (Barber et al. 2006).

Craig et al. (2006) demonstrated that populations of a common grouper (the flag cabrilla, *Epinephelus labriformis*; Epinephelidae) are genetically homogeneous across two faunal transition zones in the tropical Eastern Pacific. Despite long stretches of sandy shoreline and the absence of appropriate reef habitat, the species is able to maintain strong genetic connectivity across these coastal barriers. In contrast, a genetic break is apparent between coastal habitats and peripheral insular locations (Clipperton Island and Alijos Rocks, Baja Sur). These and other examples provide useful information in the context of conservation biology: if decisions were made based on the assumption that genetic breaks correspond primarily to faunal breaks, the presence of unique populations (or species) would likely be missed.

### Ecology and phylogeography

If one of the goals of conservation biology is to identify and preserve areas of endemism (the so-called biodiversity “hotspots”), where should we look for such endemism: In geographically isolated locations or among locations with divergent ecological conditions? To date, the identification of such hotspots has relied primarily on geography, and is largely based on taxonomy and species distributions (Roberts et al. 2002; Lourie and Vincent 2004b). However, ecological processes influence marine evolution as well (Rocha et al. 2005a; Conover et al. 2006; Choat 2006), and may indicate the necessity of identifying “ecological hotspots.”

Undeniably, biogeographical barriers and geographical isolation greatly influence diversification on coral reefs. However, the previous section indicates that there are only a handful of such readily recognizable barriers in the sea; yet, coral reefs harbour one of the most diverse assemblages of organisms on earth. This observation defies explanation with the most accepted mechanism of diversification: allopatric speciation, or speciation due to geographic isolation (Mayr 1963; Coyne and Orr 2004). The alternatives, speciation with complete (sympatric) and partial (parapatric) range overlap, have been proposed for several terrestrial taxa (Schluter 2001; Doebeli and Dieckmann 2003). But how important is non-allopatric speciation in generating and maintaining biodiversity in the sea? Recent studies in corals, sponges, molluscs and fishes indicate that natural selection can strongly influence diversification processes, and ultimately may be as important as geography in driving speciation.

Two sympatric morphotypes of the coral species *Favia fragum* in Panama revealed strong evidence for an impor-

tant role of natural selection in coral speciation. The two types have significant genetic differences yet co-occur in the same reefs. However, one of the types prefers shallower waters subjected to strong fluctuations in salinity and turbidity and the other inhabits a deeper and more stable environment. The differences persist even in the face of gene flow among types, and are apparently maintained by strong natural selection (Carlson and Budd 2002). At the Great Barrier Reef, population structure in the reef-building coral *Acropora millepora* is strongly associated with water temperature (Smith-Keune and van Oppen 2006). The marine sponge *Chondrilla* cf. *nucula* exhibits significant genetic difference between adjacent mangrove and reef populations, but remarkable similarity among widely separated populations occupying the same habitat (Duran and Rützler 2006). In Indo-Pacific snails of the genus *Echinolittorina*, genetic breaks correspond not only to the Sunda shelf region, but also to the ecological discontinuity between continental and insular environments (Reid et al. 2006). Finally, in coral dwelling nudibranchs of the genus *Phestilla*, genetic partitions sort according to coral host and not to geography (Fauci et al. 2007).

In Atlantic reef fishes, the distribution of genetic lineages of wrasses (genus *Halichoeres*) corresponds to environmental conditions and not geography; populations of *Halichoeres radiatus* in Brazilian offshore islands are more similar to those in Caribbean islands than those on the adjacent coastline (Rocha et al. 2005a), and a very similar pattern was observed in the widely distributed goby *Bathygobius soporator* (Lima et al. 2005). Deep lineages of the Atlantic parrotfish genus *Sparisoma* correspond to a shift from a coral reef to a seagrass habitat (Streelman et al. 2002). A major genetic break coinciding with abrupt changes in ecological characteristics, including temperature and salinity, separates two lineages of the eastern Pacific blenny *Axoclynus nigricaudus* within the Sea of Cortez (Riginos and Nachman 2001). In Indo-Pacific three-spot seahorses (*Hippocampus trimaculatus*) the difference among populations separated by an apparent ecological barrier (continental versus insular habitats) is greater than that between populations separated by the Sunda shelf barrier (Lourie and Vincent 2004a). Finally, compelling evidence for sympatric speciation was demonstrated in gobies of the genus *Gobiodon*, wherein species level separations do not follow geography, but shifts in the coral host (Munday et al. 2004).

These and other examples have led to the recognition of environmental variation and natural selection as powerful forces driving population structure (Choat 2006). Thus, resource managers should aim to design marine reserve networks considering not only geography, but also ecological partitions. Even though areas in close geographic proximity (such as oceanic islands and the adjacent coastline) may

appear strongly connected by currents, these communities are ecologically (and many times genetically) so different that they should be treated as separate and independent management units. Ultimately, both natural selection and geography shape the genetic architecture of marine species, and neither should be neglected. Phylogeographic studies that sample through an appropriate geographic scale (ideally the entire species range) and through habitats with different ecological characteristics (such as oceanic and continental, or tropical and subtropical locations) have a much greater chance of detecting evolutionarily significant units and pointing towards appropriate conservation measures.

### When genetics contradicts taxonomy

Prior to discussing problems related to taxonomy, and since the term species will be used frequently below, it is appropriate to provide a definition of the term. In recent years, the species concept debate started to point towards the idea that species are simply evolving lineages or evolving populations (Avise and Wollenberg 1997; Hey et al. 2003). De Queiroz (1998) pointed out that conflicts between species concepts exist because different concepts apply to different stages in the speciation process, for example a species may pass through a “phylogenetic species” (reciprocally monophyletic lineages) stage before becoming a “biological species” (reproductively isolated units). Since the speciation process consists of a continuum, the operational question of when these units should be formally named often rests on the shoulders of taxonomists. In this section we will discuss discrepancies between genetically diagnosable units and formally named species, thus the only applicable species concept in this discussion is the one most often used by taxonomists when describing species, the morphological concept. Therefore, the term “species” will be used to refer to morphologically diagnosable units named and recognized by taxonomists.

Most contemporary phylogeographic surveys involve genetic markers that are not linked to morphology (usually mitochondrial DNA segments). These markers are useful for investigating historical processes within species, as well as evolutionary relationships among species. However, mutational changes occur everywhere in the genome, and natural selection can quickly increase the frequency of advantageous (or decrease that of deleterious) mutations. If those mutations occur in genes that control easily recognizable morphological characters (such as colour and body shape) and are driven to fixation by selection, they can quickly create distinct populations (Losos et al. 1998; Endler et al. 2005) that do not differ at mtDNA sequences. Likewise, if selection acts to maintain morphological

characters, species that have been genetically separated for millions of years can be indistinguishable to the human eye (Santos et al. 2006; Bowen et al. in press).

Since the overwhelming majority of species descriptions are based exclusively on morphology, the main reason why population genetic and molecular systematic studies often contradict well-established taxonomy is because rates of evolution of morphological characters that are under the influence of selection are decoupled from the rates of molecular evolution at mtDNA genes used in genetic surveys. Characters such as colour pattern may thus show patterns of divergence that precede genetic divergence at mtDNA loci (Craig et al. 2006). Phylogeography thus aims to represent the historical trajectory of the species, whereas morphology reflects adaptations, and these two are often discordant. This creates two problems that have direct effect on the conservation of coral reef organisms: (1) The lack of taxonomic recognition and consequent oversight of genetically unique evolutionary units (cryptic species), and (2) The separation of genetically homogenous but morphologically variable species into several taxonomic units (taxonomically recognized populations). Examples of both are common in coral reefs and are discussed in detail below.

### Cryptic speciation

The subject of cryptic or sibling species in the sea was reviewed by Knowlton (1993, 2000), and here we will concentrate on the most recent developments in the area. The identification of sibling or cryptic species (species that are morphologically identical, but represent distinct evolutionary lineages; Knowlton 1993; Brown and Lomolino 1998) within a morpho-species represents an important by-product of phylogeography studies. Often, it is assumed that across the range of a morphologically homogeneous and widely distributed species, intraspecific gene genealogies should be shallow, or geographically differentiated at a population level (i.e. allele frequency shifts). Genetic homogeneity is observed in species with high dispersal potential, such as the surgeonfishes *Acanthurus triostegus*, *Acanthurus chirurgus*, and *Naso vlamingii* (Planes and Fauvelot 2002; Rocha et al. 2002; Klanten et al. 2007), the soldierfishes (genus *Myripristis*; Bowen et al. 2006b; Craig et al. 2007), pygmy angelfishes (genus *Centropyge*; Bowen et al. 2006a; Schultz et al. 2007), Pacific gobies (genus *Gnatholepis*; Thacker 2004) and a few other species that are able to cross the eastern Pacific barrier (Lessios and Robertson 2006). However, they seem to be exceptions, and numerous examples have shown that the presence of deep genetic breaks (i.e. numerous fixed mutations separating populations) within widely distributed coral reef species is more common than previously thought. Indeed, 8 of

15 reef fishes surveyed in the Atlantic showed evidence of cryptic species (Bowen et al. 2006b and references therein). The implications of these findings are a subject of much debate. Do these lineages represent management units, evolutionarily significant units (*sensu* Moritz 1994), sub-species, or cryptic species? Conservation efforts often consider genetic divergence based upon phylogenetic criteria (Mace et al. 2003), so the rank that we apply to these lineages may alter conservation priorities.

Bonefishes (genus *Albula*) live in tropical shallow waters over sand flats, usually close to coral reefs. They are part of an ancient and unique lineage, containing only a handful of species and located at the base of the tree of bony fishes (Nelson 2006). Since taxonomic distinctiveness and uniqueness are important when setting conservation goals (US Fish and Wildlife Service 1983), the bonefishes are a priority. However, until recently, the shallow water bonefishes distributed from the Caribbean, through the Indian and western Pacific Ocean and to the Central Pacific, were considered to be a single homogeneous species, *Albula vulpes*, and were managed as such. A recent mtDNA survey revealed that the once circum-tropical bonefish consists of perhaps ten genetic lineages, or cryptic species, and many unique populations. As a result, bonefish from all over the world are receiving new (or revalidated) names and being managed as separate species (Pfeiler et al. 2002; Bowen et al. 2007; Friedlander et al. in 2007; Pfeiler et al. 2006).

Other examples come from sharks and reef fishes: a study that examined intraspecific genetic variation in hammerhead sharks (*Sphyrna lewini*; Sphyrnidae) found that all of the South Atlantic, Indian Ocean, and Pacific populations are very similar, however, a unique population in the north-western Atlantic appears to represent a cryptic and

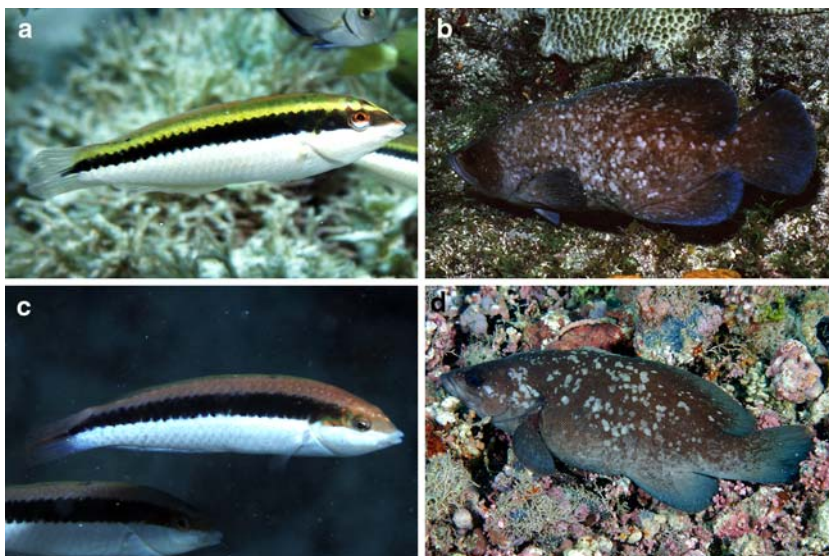
previously undetected species (Duncan et al. 2006; Quattro et al. 2006). Numerous wrasses and parrotfishes in the western Atlantic were considered to be widely distributed species with slightly different populations in the Caribbean and Brazil, separated by the Amazon barrier (Fig. 2). Recent phylogeographic surveys indicate that these populations actually represent deeply divergent lineages, which are now recognized as valid species (Rocha 2004; Robertson et al. 2006). Populations of the soapfish *Rypticus saponaceus* on either side of the Atlantic (Fig. 2) are separated by a 4.1% sequence divergence at the cytochrome *b* mtDNA gene (Carlin et al. 2003). The red lip blenny, *Ophioblennius atlanticus*, is composed of five genetic lineages within the Atlantic, each corresponding to a major zoogeographic region (Muss et al. 2001). In the Indo-Pacific, Messmer et al. (2005) detected species level mtDNA (control region) divergences among three populations of *Pseudochromis fuscus* separated by weak barriers (short open-ocean distances, freshwater, and sediment discharges from rivers); and species level separations in two mtDNA loci (cytochrome *b* gene and D-loop) among populations of the brooding damselfish *Acanthochromis polyacanthus* were observed in a short geographical scale within the Great Barrier Reef in Australia, and between the GBR and the Coral Sea (Planes et al. 2001; Bay et al. 2006).

The phenomenon is not unique to fishes; a recent survey of the sea anemone *Actinia equina* shows divergent genetic lineages that should be treated as separate species (Schama et al. 2004). A genetic survey of eastern Pacific sea urchins revealed that the widely distributed *Eucidaris thouarsi* is composed of two deeply separated lineages, one restricted to oceanic islands and another occurring along the coast (Lessios et al. 1999); and in the urchin genus *Diadema* several deeply divergent and previously undetected clades,

**Fig. 2** Cryptic species detected by genetic markers.

**a** *Halichoeres maculipinna* from the Caribbean, and **b** *Rypticus saponaceus* from Brazil.

**c** *Halichoeres penrosei* from Brazil are separated by a mean sequence divergence of 6.5% at the cytochrome *b* mtDNA gene, and **d** West Africa are separated by a mean sequence divergence of 4.1% at the cytochrome *b* mtDNA gene



were identified in the Atlantic and Pacific oceans (Lessios et al. 2001). Brazilian and Caribbean populations of spiny lobster (*Panulirus argus*, a species with very high commercial value and widely exploited throughout its range) represent two cryptic species treated as a single taxonomic unit (Sarver et al. 1998). In groups where morphology does not provide reliable characters, such as in marine sponges, phylogeographic surveys are expected to reveal many cryptic species (Lazoski et al. 2001; Wörheide et al. 2005). But perhaps the most extreme example of undetected cryptic speciation comes from an Indo-Pacific turbinid gastropod: Meyer et al. (2005) surveyed populations of the widely distributed *Astrarium rhodostomum*, and this “species” is comprised of at least 30 divergent genetic lineages, each inhabiting a different archipelago, sometimes separated by only a few hundred kilometres. It is important to stress that sharp breaks in fast evolving mtDNA loci may arise randomly, and before any taxonomic decision is made, genealogical concordance across multiple loci (preferably mtDNA and nuclear DNA) is necessary (Kuo and Avise 2005).

The identification of discrete genetic lineages within a widely distributed species is often followed by the discovery of previously unobserved morphological differentiation (genealogical concordance), and subsequent recognition of the lineages as valid species. Hence there is a growing recognition that the application of phylogeographical data may also increase our awareness of the net biodiversity in the marine environment. As many conservation priorities are based on observable biodiversity units, these data often have profound implications for management priorities. Moreover, even when genetic surveys do not result in taxonomic reshuffling, data from comparative phylogeography studies are starting to identify areas of genetic endemism and can ultimately help coastal and oceanic nations decide where to focus their conservation efforts.

#### Taxonomically recognized populations

Although less common than the discovery of cryptic species, it is not rare to find studies that show great genetic similarity between recognized species. In a phylogeographic survey of sea turtles (genus *Chelonia*), Karl and Bowen (1999) observed no genetic distinction between the green sea turtle (*Chelonia mydas*; found in all tropical seas) and the black sea turtle (*Chelonia agassizi*; restricted to the tropical eastern Pacific). Even though their conclusion was that these two species should be treated as a single taxon, they recommended that special conservation measures should be applied to the black turtle, as it possesses unique morphological characters not yet reflected in mitochondrial DNA markers.

Likewise, three recognized species of Atlantic pygmy angelfishes widely exploited by the aquarium trade (*Centropyge aurantonotus* in Brazil, *Centropyge argi* in the Caribbean and *Centropyge resplendens* in the central Atlantic; Fig. 3) show distinctive colour differences but no genetic difference in mtDNA sequences. The explanation lies again in the rates of DNA evolution: a comparison with the Indian Ocean *Centropyge acanthops* revealed that the ancestor of these three species likely invaded the Atlantic in the last 250 thousand years (Bowen et al. 2006a). Each of the three populations possesses a distinct colour pattern, however, no genetic difference was detected because there was insufficient time for mutations to accumulate in the mtDNA markers surveyed, a pattern also observed in a Pacific pygmy angelfish (Schultz et al. 2007). As we do not know what would happen if those populations were brought back into contact, only time will tell if they retain separate evolutionary paths.

Discordance between colour based taxonomy and population genetics data are also apparent in Caribbean hamlets (fishes of the genus *Hypoplectrus*, Fig. 3), Indo-Pacific damselfishes (genus *Dascyllus*) and some Pacific butterflyfishes (genus *Chaetodon*). In hamlets, the taxonomic richness (seven recognized species and two additional unnamed colour morphs) is higher and the geographical scale (Caribbean region) is smaller than in pygmy angelfishes, making the group even more remarkable. Two explanations, both involving recent diversification, have been proposed: first, divergence could be driven by adaptation to slightly different reef habitats, with an apparent signal of historical hybridization among colour morphs (McCartney et al. 2003; Ramon et al. 2003). Second, disruptive natural selection on colour, reinforced by assortative mating may maintain colour polymorphisms (Puebla et al. 2007). In damselfishes of the genus *Dascyllus*, and some butterflyfishes of the genus *Chaetodon*, the distribution of genetic lineages is largely incongruent with accepted species boundaries (McMillan et al. 1999; Bernardi et al. 2002; McCafferty et al. 2002). Examples are common also in invertebrates; current taxonomy in the sea anemone genus *Actinia* is strongly discordant with genetic partitions (Schama et al. 2004) and the two recognized Atlantic species of the sea urchin genus *Eucidaris* have no detectable mtDNA differences (Lessios et al. 1999).

Regardless of the level of genetic variation at mtDNA loci, the majority of these studies concluded that species with no genetic differences are distinguished by subtle and diagnostic colouration and/or morphology. Hence they probably are not connected at an ecological time-scale and should continue to be treated as distinct units for management purposes at least until more detailed studies of phenotypic variation are carried out (Conover et al. 2006).

**Fig. 3** Recognized species that show no genetic difference at neutral DNA markers. The hamlets **a** *Hypoplectrus puella*, **b** *Hypoplectrus nigricans*, and **c** *Hypoplectrus indigo*; and the pygmy angelfishes **d** *Centropyge argi*, **e** *Centropyge aurantonotus*, and **f** *Centropyge resplendens*



## Future

The front line in marine conservation genetics is the proper identification of management units, and phylogeography offers great help in identifying such units. Genetic surveys have the potential to reveal isolated and unique lineages (cryptic species), as well as to inform us which recognized species correspond to ancient or recently diverged populations. Biogeographic barriers provide an excellent starting point for population genetic surveys; however, in order to identify as many unique populations as possible and adequately protect them, it is necessary to survey the entire geographical and ecological range of each putative species. To date, phylogeographic surveys have revealed many deep lineages (cryptic species and evolutionary significant units) as well as isolated populations (stocks and management units) in coral reef organisms.

In addition, we must also identify the processes that produce future biodiversity (Bowen and Roman 2005). For example the evolutionary history of goldspot gobies (*Gnatholepis thompsoni*) and pygmy angelfishes (genus *Centropyge*) indicate that global warming may re-open connections between the tropical Atlantic and Indian Oceans (Rocha et al. 2005b; Bowen et al. 2006a). Even though faunal exchanges between these regions occurred naturally in the past, consequences from a human-induced opening are unpredictable. Artificial gene flow induced by

ship ballast water also represents a problem for marine populations (Carlton and Geller 1993) because it can break down genetic differences that have been accumulating for millions of years. Thus, because the populations of today potentially are the species of the future, genetic connections (or lack thereof) among them must be effectively protected. Phylogeography assumes a central role in identifying such populations.

The tools most commonly used in phylogeography (mtDNA markers) suffer from two main limitations. First, mtDNA seems to easily flow between some species in reef fish hybrid zones (van Herwerden and Doherty 2006; van Herwerden et al. 2006; Yaakub et al. 2006) and the genetic pattern observed in some populations may not correspond to the species evolutionary history, but merely to the history of the mitochondria (Ballard and Whitlock 2004). However, since most phylogeography studies involve the analysis of hundreds of sequences across the entire species range (Avice 2000), the presence of highly divergent mtDNA types within species is relatively easy to detect. Nonetheless, the interpretation of mtDNA data alone should be done with caution, especially if hybridization is suspected, and in such cases nuclear DNA should be analysed in conjunction with mtDNA (Bowen et al. 2005; van Herwerden et al. 2006).

Second, the resolution of currently used DNA markers is limited and they are not useful in cases where differentiation



is recent and driven by adaptation or strong selection. For example, many studies have tried to find genetic differences among nominal species of hamlets (Fig. 3), and those based on allozymes and mtDNA have found none (Graves and Rosenblatt 1980; Domeier 1994; Ramon et al. 2003). Microsatellites may help solve this problem (Puebla et al. 2007), and their use is increasing in phylogeography and connectivity surveys (Hoffman et al. 2005; Purcell et al. 2006; Hellberg 2007). However, the ability to detect emerging species may ultimately come from the analysis of genes that are directly under the influence of selection (Conover et al. 2006). Whitehead and Crawford (2006) demonstrated that, although no differences are observed at a range of DNA loci among populations of the fish *Fundulus heteroclitus*, there is a significant shift in metabolic gene expression between populations in cold and warm temperatures. Since most reef fish are restricted to the warm tropical region, temperature-related gene expression analyses would not be the priority in these systems, however, a revolution in studies of reef fish phylogeography and evolution could start with the genes that code for and regulate the expression of colour. Colour is among the most conspicuous characters in several reef fish families, and is used by them in many ways, including mate recognition, aggressive behaviour, social systems, mimicry, camouflage, etc. As more genomes are sequenced and more genes are mapped, the potential breakthrough of utilizing “colour genes” in studies of reef fish phylogeography and evolution comes closer to reality.

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## References

- Avice JC (1992) Molecular population structure and the biogeographic history of a regional fauna: a case history with lessons for conservation biology. *Oikos* 63:62–76
- Avice JC (2000) *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge
- Avice JC, Ball RM (1990) Principles of genealogical concordance in species concepts and biological taxonomy. In: Futuyma DJ, Antonovics J (eds) *Oxford surveys in evolutionary biology*. Oxford University Press, Oxford, pp 45–67
- Avice JC, Wollenberg K (1997) Phylogenetics and the origin of species. *Proc Natl Acad Sci USA* 94:7748–7755
- Ballard JWO, Whitlock MC (2004) The incomplete natural history of mitochondria. *Mol Ecol* 13:729–744
- Barber PH, Bellwood DR (2005) Biodiversity hotspots: evolutionary origins of biodiversity in wrasses (*Halichoeres*: Labridae) in the Indo-Pacific and new world tropics. *Mol Phylogenet Evol* 35:235–253
- Barber PH, Erdmann MV, Palumbi SR (2006) Comparative phylogeography of three codistributed stomatopods: origins and timing of regional lineage diversification in the coral triangle. *Evolution* 60:1825–1839
- Baums IB, Paris CB, Cherubin LM (2006) A bio-oceanographic filter to larval dispersal in a reef-building coral. *Limnol Oceanogr* 51:1969–1981
- Bay LK, Choat JH, van Herwerden L, Robertson DR (2004) High genetic diversities and complex genetic structure in an Indo-Pacific tropical reef fish (*Chlorurus sordidus*): evidence of an unstable evolutionary past? *Mar Biol* 144:757–767
- Bay LK, Crozier RH, Caley MJ (2006) The relationship between population genetic structure and pelagic larval duration in coral reef fishes on the Great Barrier Reef. *Mar Biol* 149:1247–1256
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Bermingham E, McCafferty SS, Martin AP (1997) Fish biogeography and molecular clocks: perspectives from the Panamanian Isthmus. In: Kocher TD, Stepien CA (eds) *Molecular systematics of fishes*. Academic, New York, pp 113–128
- Bernardi G, Lape J (2005) Tempo and mode of speciation in the Baja California disjunct fish species *Anisotremus davidsonii*. *Mol Ecol* 14:4085–4096
- Bernardi G, Holbrook SJ, Schmitt RJ, Crane NL, DeMartini E (2002) Species boundaries, populations and colour morphs in the coral reef three-spot damselfish (*Dascyllus trimaculatus*) species complex. *Proc R Soc Lond B* 269:599–605
- Bernardi G, Findley L, Rocha-Olivares A (2003) Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution* 57:1599–1609
- Bowen BW, Roman J (2005) Gaia’s handmaidens: the Orlog model for conservation. *Conserv Biol* 19:1037–1043
- Bowen BW, Bass AL, Soares L, Toonen RJ (2005) Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). *Mol Ecol* 14:2389–2402
- Bowen BW, Muss A, Rocha LA, Grant WS (2006a) Shallow mtDNA coalescence in Atlantic pygmy angelfishes (Genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *J Hered* 97:1–12
- Bowen BW, Bass AL, Muss A, Carlin JL, Robertson DR (2006b) Phylogeography of two Atlantic squirrelfishes (Family Holocentridae): exploring links between pelagic larval duration and population connectivity. *Mar Biol* 149:899–913
- Bowen BW, Karl SA, Pfeiler E (2007) Resolving evolutionary lineages and taxonomy of bonefishes (*Albula* spp.). In: Ault JS (ed) *Biology and management of the world tarpon and bonefish fisheries*. CRC, Boca Raton, in press
- Briggs JC (1974) *Marine zoogeography*. McGraw-Hill, New York
- Brown JH, Lomolino MV (1998) *Biogeography*. Sinauer Associates Inc., Sunderland
- Burton RS (1998) Intraspecific phylogeography across the point conception biogeographic boundary. *Evolution* 52:734–745
- Carlin JL, Robertson DR, Bowen BW (2003) Ancient divergences and recent connections in two tropical Atlantic reef fishes: *Epinephelus adscensionis* and *Rypticus saponaceus* (Percoidae: Serranidae). *Mar Biol* 143:1057–1069
- Carlson DB, Budd AF (2002) Incipient speciation across a depth gradient in a scleractinian coral? *Evolution* 56:2227–2242
- Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261:78–82
- Choat H (2006) Phylogeography and reef fishes: bringing ecology back into the argument. *J Biogeogr* 33:967–968
- Conover DO, Clarke LM, Munch SB, Wagner GN (2006) Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation. *J Fish Biol* 69(Suppl C):21–47

- Coyne JA, Orr HA (2004) Speciation. Sinauer Associates Inc., Sunderland
- Cowen RK (2002) Larval dispersal and retention, and consequences for population connectivity. In: Sale PF (ed) Coral reef fishes. Dynamics and diversity in a complex ecosystem. Academic, New York, pp 149–170
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522–527
- Craig MT, Hastings PA, Pondella II DJ, Robertson DR, Casian JAR (2006) Phylogeography of the flag cabrilla (*Epinephelus labriformis*, Serranidae): implications for the biogeography of the tropical eastern Pacific and the early stages of speciation in a marine shore fish. *J Biogeogr* 33:969–979
- Craig MT, Eble JA, Robertson DR, Bowen BW (2007) High genetic connectivity across the Indian and Pacific Oceans in the reef fish *Myripristis berndti* (Holocentridae). *Mar Ecol Prog Ser* 334:245–254
- De Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation. In: Howard DJ, Berlocher SH (eds) Endless forms: species and speciation. Oxford University Press, New York, pp 57–75
- Doebeli M, Dieckmann U (2003) Speciation along environmental gradients. *Nature* 421:259–264
- Domeier ML (1994) Speciation in the serranid fish *Hypoplectrus*. *Bull Mar Sci* 54:103–141
- Duncan KM, Martin AP, Bowen BW, De Couet HG (2006) Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). *Mol Ecol* 15:2239–2251
- Duran S, Rützler K (2006) Ecological speciation in a Caribbean marine sponge. *Mol Phylogenet Evol* 40:292–297
- Ekman S (1953) Zoogeography of the sea. Sidgwick and Jackson, London
- Endler JA, Wescotte DA, Madden JR, Robson T (2005) Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution* 59:1795–1818
- Fauci A, Toonen RJ, Hadfield MG (2007) Host shift and speciation in a coral-feeding nudibranch. *Proc R Soc Lond B* 274:111–119
- Friedlander A, Caselle JE, Beets J, Lowe C, Bowen BW, Ogawa T, Kelly K, Calitri T, Lange M, Anderson B (2007) Aspects of the biology, ecology, and recreational fishery for bonefish at Palmyra Atoll National Wildlife Refuge, with comparisons to other Pacific Islands. In: Ault JS (ed) Biology and management of the world tarpon and bonefish fisheries. CRC, Boca Raton, in press
- Graves JE, Rosenblatt RH (1980) Genetic relationships of the color morphs of the serranid fish *Hypoplectrus unicolor*. *Evolution* 34:240–245
- Halpern BS, Regan HM, Possingham HP, McCarthy MA (2006) Accounting for uncertainty in marine reserve design. *Ecol Lett* 9:2–11
- Hastings PA (2000) Biogeography of the tropical eastern Pacific: distribution and phylogeny of chaenopsid fishes. *Zool J Linn Soc* 128:319–335
- Hastings PA, Springer VG (1994) Review of *Stathmonotus*, with redefinition and phylogenetic analysis of the Chaenopsidae (Teleostei: Blennioidei). *Smithson Contrib Zool* 558:1–48
- Hellberg M (2007) Footprints on water: the genetic wake of dispersal among reefs. *Coral Reefs* (this issue)
- Hey J, Waples RS, Arnold ML, Butlin RK, Harrison RG (2003) Understanding and confronting species uncertainty in biology and conservation. *Trends Ecol Evol* 18:597–603
- Hoffman EA, Kolm N, Berglund A, Arguello JR, Jones AG (2005) Genetic structure in the coral-reef-associated Banggai cardinalfish, *Pterapogon kauderni*. *Mol Ecol* 14:1367–1375
- Karl SA, Bowen BW (1999) Evolutionary significant units versus geopolitical taxonomy: molecular systematics of an endangered sea turtle (genus *Chelonia*). *Conserv Biol* 13:990–999
- Klanten SE, Choat H, van Herwerden L (2007) Extreme genetic diversity and temporal rather than spatial partitioning in a widely distributed coral reef. *Mar Biol* 150:659–670
- Knowlton N (1993) Sibling species in the sea. *Annu Rev Ecol Syst* 24:189–216
- Knowlton N (2000) Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* 420:73–90
- Knowlton N, Weigt LA (1998) New dates and new rates for divergence across the Isthmus of Panama. *Proc R Soc Lond B* 265:2257–2263
- Kuo CH, Avise JC (2005) Phylogeographic breaks in low-dispersal species: the emergence of concordance across gene trees. *Genetica* 124:179–186
- Lazoski C, Solé-Cava AM, Boury-Esnault N, Klautau M, Russo CAM (2001) Cryptic speciation in a high gene flow scenario in the oviparous marine sponge *Chondrosia reniformis*. *Mar Biol* 139:421–429
- Leis JM (2002) Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. *Env Biol Fishes* 65:199–208
- Lessios HA, Robertson DR (2006) Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proc R Soc Lond B* 273:2201–2208
- Lessios HA, Kessing BD, Robertson DR, Paulay G (1999) Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution* 53:806–817
- Lessios HA, Kessing BD, Pearse JS (2001) Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution* 55:955–975
- Lima D, Freitas JEP, Araujo ME, Solé-Cava AM (2005) Genetic detection of cryptic species in the frillfin goby *Bathygobius soporator*. *J Exp Mar Biol Ecol* 320:211–223
- Losos JB, Jackman TR, Larson A, de Queiroz K, Rodriguez-Schettino L (1998) Contingency and determinism in replicated adaptive radiations of Island lizards. *Science* 279:2115–2118
- Lourie SA, Vincent ACJ (2004a) A marine fish follows Wallace's Line: the phylogeography of the three-spot seahorse (*Hippocampus trimaculatus*, Syngnathidae, Teleostei) in Southeast Asia. *J Biogeogr* 31:1975–1985
- Lourie SA, Vincent ACJ (2004b) Using biogeography to help set priorities in marine conservation. *Conserv Biol* 18:1004–1020
- Mace GM, Gittleman JL, Purvis A (2003) Preserving the tree of life. *Science* 300:1707–1709
- Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge
- McCafferty S, Bermingham E, Quenouille B, Planes S, Hoelzer G, Asoh K (2002) Historical biogeography and molecular systematics of the Indo-Pacific genus *Dascyllus* (Teleostei: Pomacentridae). *Mol Ecol* 11:1377–1392
- McCartney MA, Acevedo J, Heredia C, Rico C, Quenouille B, Bermingham E, McMillan WO (2003) Genetic mosaic in a marine species flock. *Mol Ecol* 12:2963–2973
- McMillan WO, Weigt LA, Palumbi SR (1999) Color pattern evolution, assortative mating, and genetic differentiation in brightly colored butterflyfishes (Chaetodontidae). *Evolution* 53:247–260
- Messmer V, van Herwerden L, Munday PL, Jones GP (2005) Phylogeography of colour polymorphism in the coral reef fish *Pseudochromis fuscus*, from Papua New Guinea and the Great Barrier Reef. *Coral Reefs* 24:392–402
- Meyer CP, Geller JB, Paulay G (2005) Fine scale endemism on coral reefs: archipelagic differentiation in turbinid gastropods. *Evolution* 59:113–125
- Mora C, Sale PF (2002) Are populations of coral reef fish open or closed? *Trends Ecol Evol* 17:422–428
- Mora C, Andréfouët S, Costello MJ, Kranenburg C, Rollo A, Veron JE, Gaston KJ, Myers RA (2006) Coral reefs and the global network of marine protected areas. *Science* 312:1750–1751

- Moritz C (1994) Defining “evolutionary significant units” for conservation. *Trends Ecol Evol* 9:373–375
- Moritz C, Faith DP (1998) Comparative phylogeography and the identification of genetically divergent areas for conservation. *Mol Ecol* 7:419–429
- Munday PL, van Herwerden L, Dudgeon CL (2004) Evidence for sympatric speciation by host shift in the sea. *Curr Biol* 14:1498–1504
- Muss A, Robertson DR, Stepien CA, Wirtz P, Bowen BW (2001) Phylogeography of *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution* 55:561–572
- Nelson JS (2006) *Fishes of the world*. Wiley, New York
- Palumbi SR (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annu Rev Environ Resour* 29:31–68
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Paulay G, Meyer A (2006) Dispersal and divergence across the greatest ocean region: do larvae matter? *Integr Comp Biol* 46:269–281
- Pfeiler E, Colborn J, Douglas MR, Douglas ME (2002) Systematic status of the bonefishes (*Albula* spp.) from the eastern Pacific Ocean inferred from analyses of allozymes and mitochondrial DNA. *Environ Biol Fish* 63:151–159
- Pfeiler E, Bitler BG, Ulloa R (2006) Phylogenetic relationships of the shafted bonefish *Albula nemoptera* (Albuliformes: Albulidae) from the eastern Pacific based on cytochrome *b* sequence analysis. *Copeia* 2006:778–784
- Planes S, Fauvelot C (2002) Isolation by distance and vicariance drive genetic structure of a coral reef fish in the Pacific Ocean. *Evolution* 56:378–399
- Planes S, Doherty PJ, Bernardi G (2001) Strong genetic divergence among populations of a marine fish with limited dispersal, *Acanthochromis polyacanthus*, within the Great Barrier Reef and the Coral Sea. *Evolution* 55:2263–2273
- Puebla O, Bermingham E, Guichard F, Whiteman E (2007) Colour pattern as a single trait driving speciation in *Hypoplectrus* coral reef fishes? *Proc R Soc Lond B* 274:1265–1271
- Purcell JFH, Cowen RK, Hughes CR, Williams DA (2006) Weak genetic structure indicates strong dispersal limits: a tale of two coral reef fish. *Proc R Soc Lond B* 273:1483–1490
- Quattro JM, Stoner DS, Driggers WB, Anderson CA, Priede KA, Hoppmann EC, Campbell NH, Duncan KM, Grady JM (2006) Genetic evidence for cryptic speciation within hammerhead sharks (Genus *Sphyrna*). *Mar Biol* 148:1143–1155
- Ramon ML, Lobel PS, Sorenson MD (2003) Lack of mitochondrial genetic structure in hamlets (*Hypoplectrus* spp.): recent speciation or ongoing hybridization? *Mol Ecol* 12:2975–2980
- Randall JE (1998) Zoogeography of shore fishes of the Indo-Pacific region. *Zool Stud* 37:227–268
- Reid DG, Lal K, Mackenzie-Dodds J, Kaligis F, Littlewood DTJ, Williams ST (2006) Comparative phylogeography and species boundaries in *Echinolittorina* snails in the central Indo-West Pacific. *J Biogeogr* 33:990–1006
- Riginos C (2005) Cryptic vicariance in Gulf of California fishes parallels vicariant patterns found in Baja California mammals and reptiles. *Evolution* 59:2678–2690
- Riginos C, Nachman MW (2001) Population subdivision in marine environments: the contributions of biogeography, geographical distance and discontinuous habitat to genetic differentiation in a blennioid fish, *Axoclinus nigricaudus*. *Mol Ecol* 10:1439–1453
- Riginos C, Victor B (2001) Larval spatial distributions and other early life-history characteristics predict genetic differentiation in eastern Pacific blennioid fishes. *Proc R Soc Lond B* 268:1931–1936
- Roberts CM, McClean CJ, Veron JE, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Wynne C, Werner TB (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295:1280–1284
- Robertson DR, Karg F, de Moura RL, Victor B, Bernardi G (2006) Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Mol Phylogenet Evol* 40:795–807
- Rocha LA (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. *J Biogeogr* 30:1161–1171
- Rocha LA (2004) Mitochondrial DNA and color pattern variation in three western Atlantic *Halichoeres* (Labridae), with the revalidation of two species. *Copeia* 2004:770–782
- Rocha LA, Bass AL, Robertson DR, Bowen BW (2002) Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Mol Ecol* 11:243–252
- Rocha LA, Robertson DR, Roman J, Bowen BW (2005a) Ecological speciation in tropical reef fishes. *Proc R Soc Lond B* 272:573–579
- Rocha LA, Robertson DR, Rocha CR, Van Tassell JL, Craig MT, Bowen BW (2005b) Recent invasion of the tropical Atlantic by an Indo-Pacific coral reef fish. *Mol Ecol* 14:3921–3928
- Santos S, Hrbek T, Farias IP, Schneider H, Sampaio I (2006) Population genetic structuring of the king weakfish, *Macrondon ancylodon* (Sciaenidae), in Atlantic coastal waters of South America: deep genetic divergence without morphological change. *Mol Ecol* 15:4361–4373
- Sarver SK, Silberman JD, Walsh PJ (1998) Mitochondrial DNA sequence evidence supporting the recognition of two subspecies of the Florida spiny lobster *Panulirus argus*. *J Crustacean Biol* 18:177–186
- Schama R, Solé-Cava AM, Thorpe JP (2004) Genetic divergence between east and west Atlantic populations of *Actinia* spp. sea anemones (Cnidaria: Actiniidae). *Mar Biol* 146:435–443
- Schluter D (2001) Ecology and the origin of species. *Trends Ecol Evol* 16:372–380
- Schultz JK, Pyle RL, DeMartini E, Bowen BW (2007) Genetic connectivity among color morphs and Pacific archipelagos for the flame angelfish, *Centropyge loriculus*. *Mar Biol* 151:167–175
- Shulman MJ, Bermingham E (1995) Early life histories, ocean currents and the population genetics of Caribbean reef fishes. *Evolution* 49:1041–1061
- Smith-Keune C, van Oppen MJH (2006) Genetic structure of a reef-building coral from thermally distinct environments on the Great Barrier Reef. *Coral Reefs* 25:493–502
- Streelman JT, Alfaro M, Westneat MW, Bellwood DR, Karl SA (2002) Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. *Evolution* 56:961–971
- Swearer SE, Shima JS, Hellberg ME, Thorrold SR, Jones GP, Robertson DR, Morgan SG, Selkoe KA, Ruiz GM, Warner RR (2002) Evidence of self-recruitment in demersal marine populations. *Bull Mar Sci* 70:251–271
- Taylor MS, Hellberg ME (2006) Comparative phylogeography in a genus of coral reef fishes: biogeographic and genetic concordance in the Caribbean. *Mol Ecol* 15:695–707
- Thacker CE (2004) Population structure in two species of the reef goby *Gnatholepis* (Teleostei: Perciformes) among four South Pacific Island groups. *Coral Reefs* 23:357–366
- Teske PR, McQuaid CD, Froneman PW, Barker NP (2006) Impacts of marine biogeographic boundaries on phylogeographic patterns of three South African estuarine crustaceans. *Mar Ecol Prog Ser* 314:283–293
- US Fish, Wildlife Service (1983) Endangered and threatened species listing and recovery priority guidelines. *Federal Register* 48:43098–43105
- van Herwerden L, Doherty PJ (2006) Contrasting genetic structures across two hybrid zones of a tropical reef fish, *Acanthochromis polyacanthus* (Bleeker 1855). *J Evol Biol* 19:239–252

- van Herwerden L, Choat JH, Dudgeon CL, Carlos GC, Newman SJ, Frisch A, van Oppen MJH (2006) Contrasting patterns of genetic structure in two species of the coral trout *Plectropomus* (Serranidae) from east and west Australia: introgressive hybridisation or ancestral polymorphisms. *Mol Phylogenet Evol* 41:420–435
- van Oppen MJH, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. *Mol Ecol* 15:3863–3883
- Victor BC, Wellington GM (2000) Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. *Mar Ecol Prog Ser* 205:241–248
- Whitehead A, Crawford DL (2006) Neutral and adaptive variation in gene expression. *Proc Natl Acad Sci USA* 103:5425–5430
- Wörheide G, Solé-Cava AM, Hooper JNA (2005) Biodiversity, molecular ecology and phylogeography of marine sponges: patterns, implications and outlooks. *Integr Comp Biol* 45:377–385
- Yaakub SM, Bellwood DR, van Herwerden L, Walsh FM (2006) Hybridization in coral reef fishes: introgression and bi-directional gene exchange in *Thalassoma* (family Labridae). *Mol Phylogenet Evol* 40:84–100