

## Speciation with Gene Flow in Coral Reef Fishes

Moisés A. Bernal<sup>1,2\*</sup>, Luiz A. Rocha<sup>2</sup>

<sup>1</sup> University of Texas Marine Science Institute, Port Aransas, TX 78373, USA

<sup>2</sup> Section of Ichthyology, California Academy of Sciences, San Francisco, CA 94118, USA

[bernal.moises@utexas.edu](mailto:bernal.moises@utexas.edu)

\* corresponding author

### Abstract

Recent genetic evidence has highlighted the possibility of speciation with gene flow. In marine systems, dispersive larvae accompanied by the paucity of marine barriers, greatly decrease the chances for reproductive isolation. Even when a small number of cases of speciation with gene flow have been documented in coral reef fish, this mode could represent an important alternative for explaining the observed diversity in these systems. In this work we present a brief review of the main mechanisms of speciation that operate in the marine environment, examples of groups that are known to hybridize, as well as current genetic techniques for analyzing speciation with gene flow. We give a brief explanation of the molecular work we have done so far with grunts of the *Haemulon* genus, from the Tropical Eastern Pacific and Western Atlantic. In addition, we highlight the importance of scientific diving for collections in complex environments such as coral reefs, as well as its role in allowing observation of specific behaviors that help elucidate the speciation of fishes.

Keywords: Genetics, isolation with migration, molecular evolution, natural selection, sister species, speciation genes,

### Introduction

A common reproductive strategy among marine organisms is to produce thousands of pelagic larvae with great potential for dispersal. This reduces competition and allows re-colonization of extirpated areas as well as colonization of new sites. Phylogeographic studies have demonstrated pelagic larvae can maintain genetic connectivity across the greatest oceanographic extents. This great potential for connectivity, added to the paucity of physical barriers in marine systems, raises an interesting question, how did the great diversity of coral reef fish originate?

The most “traditional” view of speciation is via allopatry. In this mode two populations are separated by a strong physical barrier that impedes reproduction. With time, the effects of mutation and drift will cause the two divergent lineages to become different species. For marine systems, one of the most famous examples is the Isthmus of Panama, where the rise of a land mass approximately 3mya divided populations in the Caribbean and Eastern Pacific (Lessios, 2008). In other cases, rare dispersal events can lead to the colonization of distant sites, which leads to restricted gene flow with central populations. This is observed in islands of the Central Pacific with high rates of endemism, such as the Hawaiian Islands, Eastern Islands and the Marquesas (Allen, 2008). Other barriers are considered “soft”, as they do not confer isolation for all species. For example, the Amazon freshwater plume causes the isolation of the surgeonfish *Acanthurus bahianus*, distributed in southern Brazil, and its sister species *Acanthurus tractus*, of the Greater Caribbean (Bernal and Rocha, 2011).

Meanwhile, the closely related *A. coeruleus* and *A. chirurgus* show no genetic structure between populations of the Caribbean and Southern Brazil (Rocha et al., 2002).

There are seven strong physical barriers that separate biogeographic provinces in coral reef systems (Rocha et al., 2007), and many more instances where local oceanographic conditions can cause isolation. However, speciation has also been demonstrated to occur in the absence of vicariance. In parapatric speciation, two populations are present in adjacent locations with different environmental conditions. Over time, the two populations become very well adapted to their local environments, which causes reproduction between individuals of the two sites less probable. Considering the vast distances and gradual changes in environmental conditions, this mode has been considered the prevalent mechanism of speciation for reef fishes (Rocha and Bowen, 2008).

Speciation can also occur when two lineages are present in the same area, that is, in sympatry. In these cases lineages become reproductively isolated by behavioral or ecological differences. Considering the low number of barriers and the potential for larval dispersal, this mode could be significantly important in reefs. Examples of this mode of speciation can be seen in wrasses (Rocha et al., 2005), gobies (Munday et al., 2004; Taylor et al., 2005), seahorses (Jones et al., 2003) and triplefins (Wellenreuther et al., 2007). However, the main issue with this mode of speciation is that it is very challenging to discern true sympatry from range expansion after allopatric speciation (Coyne and Orr, 2004).

#### ***Speciation with gene flow***

Considering the great potential for connectivity in marine systems, as well as the role of selection in parapatry and sympatry, some of the observed diversity in marine systems could occur in the presence of gene flow (Arnold and Fogherty, 2009). The main idea behind this process is that lineages are still able to diverge without genome-wide reproductive isolation. Under this scenario, genes that cause ecological, sexual or post-mating isolation can have restricted exchange in the event of hybridization between young or nascent species (speciation genes; Wu, 2001; Wu and Ting, 2004). Meanwhile, genes that have no effect on fitness may be exchanged freely between the divergent lineages. Over time, association of “speciation genes” with the rest of the genome can lead to reproductive isolation and the formation of separate species (Wu and Ting, 2004).

This mode of speciation is believed to provide a unique signal in the genome of the studied species. If enough coverage of the genome is obtained, areas under disruptive selection should show higher divergence than areas under no selection. Thus, the largest divergence between two lineages should be localized in very specific spots in the genome. Meanwhile, if species have diverged via mutations and drift, large differences should be found randomly across the entire genome. These patterns have been observed when contrasting genome scans of marine vs freshwater lineages of sticklebacks with scans of allopatric populations of the same environment (Hohenlohe et al., 2010).

#### ***Groups of Interest Among Coral Reef Fish***

In the particular case of coral reef fish, several groups have been identified as candidates for the study of hybridization and speciation with gene flow. One of the groups with most described cases corresponds to angelfishes of the Holocentridae family. Here, Pyle and Randall (1994) described 11 cases of extensive hybridization in over 5 different genera (*Apolemichthys*, *Centropyge*, *Holacanthus*, *Pomacanthus* and *Chaetodontoplus*). Following this morphological survey, genetic evidence has shown extensive introgression between different species of the genus *Centropyge* (Shultz et al., 2007; DiBattista et al., 2012). In this group species level designation corresponds to coloration, and in many instances these differences are not supported by genetic markers. The only differences at the genetic level are observed between geographic regions, where different color morphs of the same area are

more closely related than individuals of the same color morph from distant sites (DiBattista et al., 2012).

One group that has received considerable attention is the hamlets of the *Hypoplectrus* genus. The group consists of 12 species with overlapping distributions across the Tropical Western Atlantic. The species can be identified only by their coloration, as they show no differences in morphology (Fischer, 1980). Organisms preferentially mate with individuals of their same color pattern (Puebla et al., 2012), but hybridization produces viable offspring (Ramon et al., 2003, Puebla et al., 2008). Hybrid progeny have intermediate color patterns with respect to the parental morphs, which reduces the chances of successful reproduction (Puebla et al., 2012). In this case, genes that control color patterns may drive differentiation even in the presence of gene flow (Holt et al., 2011).

A group that is of particular interest for our own research is the *Haemulon* genus. The phylogeny of the group shows that physical isolation by the Isthmus of Panama and the Amazon plume played a minimal role in the radiation of the group, as most of the sister species have overlapping distributions (Rocha et al., 2008; Tavaré et al., 2012). In addition, some of the closely related species show very shallow differences with mitochondrial markers, but show substantial divergence with nuclear DNA (Rocha et al., 2008). In this case, as well as in the angelfishes and hamlets, the observed pattern could be related to rampant introgression across divergent lineages (Arnold, 2006). The difference between this and the former examples is that hybrids are not found in nature. Thus the current challenge is determining whether introgression occurred after speciation or if it was present during the divergence process.

## Discussion

The study of evolution is undergoing a rapid change mainly due to the amount of information that is now possible to obtain. With the advent of next generation sequencing there is a chance to validate potential cases of speciation with gene flow. Analyzing thousands of loci greatly enhances the possibility of understanding patterns of introgression and disruptive selection that are typical under this mode of speciation. However, it is very important to highlight that even with the advent of new sequencing techniques and powerful computer analyses, diving plays a key role for understanding speciation in coral reefs. Getting access to samples in this complex environment is routinely done with SCUBA, as collecting from the surface would result in highly un-selective sampling. Considering the available tools we have today for the study of speciation, we are confident in making progress towards a better understanding of speciation with gene flow and its relevance in marine systems in the near future.

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