Genetic Evidence for Local Retention of Pelagic Larvae in a Caribbean Reef Fish
Michael S. Taylor* and Michael E. Hellberg

The pelagic larvae of many marine organisms can potentially disperse across hundreds of kilometers, but whether oceanographic or behavioral mechanisms can constrain dispersal over periods sufficient for the evolution of genetic differentiation remains unclear. Here, we concurrently examine larval duration and genetic population differentiation in a cleaner goby, *Elacatinus evelynae*, a member of the most species-rich genus of Caribbean reef fishes. Despite evidence for extended pelagic duration (21 days), populations of *E. evelynae* show strong genetic differentiation: among color forms (1.36 to 3.04% divergent at mitochondrial cytochrome b) and among island populations within color forms (\(\Phi_{ST}\) up to 70%). These results suggest that marine populations can remain demographically closed for thousands of generations despite extended larval duration, and that recognition cues such as color may promote speciation when geographic barriers are transient or weak.

Many marine organisms have pelagic larvae that can potentially interconnect distant populations through dispersal on ocean currents. If these larvae disperse as passive propagules on advective current flow, they will be transported among both near and distant island populations (1). Species with such broadly dispersing larvae should be genetically homogeneous over large spatial scales, thus compromising their ability to adapt to local conditions (2). If, however, pelagic larvae are retained near their natal populations by behavioral (3) or physical oceanographic (4) mechanisms, then populations would have a greater opportunity for genetic differentiation and local adaptation. Should local retention persist over many generations, marine populations undivided by strong physical barriers might nonetheless form new species or at least differentiate to levels where different management or conservation strategies would be warranted for different populations.

Studies in which fluorescent tags and environmental trace elements were used as markers in otoliths—calcareous structures in the inner ear of fishes—from newly recruited juvenile fishes indicate that as many as 60% of a juvenile cohort may recruit to their natal populations, despite larval durations of 3 to 7 weeks (5, 6). However, exchange rates averaging just a single larval individual per generation among populations can be sufficient to hinder genetic differentiation caused by drift or weak selection (7). In the absence of biogeographic barriers, genetic analyses to date have failed to reveal significant population differentiation for species with broad larval-dispersal potential (8–10), including one species (bluehead wrasse, *Thalassoma bifasciatum*) shown by trace-element studies to have high larval retention (6). Here, we test for genetic differentiation among island populations separated by hundreds of kilometers in a Caribbean reef fish with pelagic larvae.

*Elacatinus (=*Gobiosoma*) evelynae*, a reef-dwelling cleaner goby, is widely distributed throughout the Bahamas and Caribbean Sea (Fig. 1). It belongs to the most species-rich genus of fishes found on west Atlantic coral reefs, as well as to the largest family of marine fishes (*Gobiidae*) (11). Although long recognized as a single species on the basis of morphological criteria (12, 13), *E. evelynae* has three brightly colored forms: yellow, blue, and white. However, individuals of the different color forms rarely co-occur, despite geographic separation by as little as 23 km.

The potential for larval dispersal between geographically proximal populations can be assessed with knowledge of currents and pelagic larval duration (PLD). Current patterns in the Caribbean have been well studied; typical current speeds average 1 to 2 km/hour (4). We determined PLD for *E. evelynae* by counting daily growth rings in the otoliths from the core (which forms as the planktonic stage begins after hatching) to the settlement check (which forms as the planktonic stage ends and individuals settle onto the reef) (14). Larvae of all color forms had a PLD of about 3 weeks (Table 1); the mean PLD of the yellow form (25 days) was slightly longer than that of blue or white forms (21 days; \(P < 0.001\)). Assuming passive dispersal and a conservatively estimated current speed of 1 km/hour (8), an individual with a 21-day PLD could potentially disperse more than 500 km per generation (corresponding to 1 year). Dispersal, however, may be influenced by factors other than PLD. Ecological requirements or behavioral attributes may cause larvae to develop near shore, rather than disperse (15). The pelagic larvae of gobies are typically found over or near reefs and not in open water (16), suggesting limited dispersal.

To assess the realized extent of genetic exchange among populations, we sampled 246 individuals from 17 Caribbean and Bahaman island populations representing all color forms (Fig. 1), and amplified and sequenced 400 base pairs of the mitochondrial cytochrome b gene by polymerase chain reaction (14). The different color forms of *E. evelynae* are genetically distinct and appear to be reproductively isolated. An analysis of molecular variation (17) indicates that 78.6% of the genetic variation is partitioned among color forms (\(\Phi_{ST}\), Table 1), and none of the 79 unique haplotypes (with the exception of 3) is shared among color forms (Fig. 2). Notably, haplotypes are not shared between blue and white forms from Puerto Rico, where they are separated by only 23 km.

Within color forms, few haplotypes are shared among populations of either the blue or the white forms, indicating that haplotypes unique to each population are not spreading (by larval dispersal to other populations. Of the 32

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**Fig. 1.** Distribution of the yellow (circles), blue (diamonds), and white (triangles) color forms of *E. evelynae* across the Bahamas and Caribbean Sea. Green squares indicate localities where both blue and yellow forms have been reported. The 17 sampled populations are indicated with red lines. Northern Bahamas represents five sampled populations (north to south): Sweetings Cay, Eleuthera Island, Lee Stocking Island, Cat Island, and Long Island. Puerto Rico represents two sampled populations, Isla Desecheo (white form) and the main island (blue form). The U.S. Virgin Islands [USVI] represents two sampled populations: St. John and St. Croix. Locality records from (12) and P.L. Colin (unpub.).
haplotypes found across blue-form populations (separated by 60 to 2000 km), only 6 occurred in more than 1 population (5 among Puerto Rico, St. John, and St. Croix, and 1 between Barbados and Grenada). Of the 19 white-form haplotypes (populations separated by 250 to 750 km), only 1 occurred in more than 1 population (Jamaica and Navassa). The blue-form populations are strongly subdivided (\(\Phi_{ST} = 0.704\); Table 1); the white form also shows considerable subdivision (\(\Phi_{ST} = 0.584\)). Furthermore, several populations within the blue form and the white form are reciprocally monophyletic (or nearly so) (Fig. 2), indicating that gene flow among populations has been absent or restricted over many generations. Using a coalescent model (14), we estimate that populations at Barbados and Curacao (separated by 1000 km) have been isolated from each other for between 75,000 and 103,000 years.

Some of the geographic subdivision we found could be due to a “sweepstakes effect,” the genetic drift among larval cohorts that results from the random reproductive success of different small subsets of adults over time. If such sweepstakes effects are important, then different larval cohorts should be genetically differentiated (18). We sampled three populations repeatedly over as many as four generations, but found no evidence of temporal subdivision that would support a reproductive sweepstakes effect (Table 2). More detailed temporal sampling of marine species that are longer lived and have overlapping generations (attributes most favorable for sweepstakes effects) have also failed to detect sweepstakes effects (19).

Our results show that strong phylogeographic structure can develop in the Caribbean Sea between marine populations separated by as little as 23 km for species that have potential for long-distance larval dispersal. The amount of genetic subdivision between populations of all three color forms (Table 1) is similar to that found between populations of an Indo-West Pacific stomatopod separated by a strong biogeographic barrier (20), where lineages with long separate histories meet; however, no such barriers are currently recognized for the Caribbean. Instead, the reciprocal monophyly of populations within the blue form and the close proximity of genetically distinct color forms observed here suggest that local larval retention generates the strong phylogeographic structure observed in *E. evelynae*.

Table 1. Mean pelagic larval duration (PLD, in days), and genetic population subdivision (\(\Phi_{ST}\)) within and among color forms.

<table>
<thead>
<tr>
<th>Color form</th>
<th>Larval duration</th>
<th>Genetic subdivision</th>
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<tbody>
<tr>
<td></td>
<td>N</td>
<td>PLD</td>
</tr>
<tr>
<td>Blue</td>
<td>48</td>
<td>21.7</td>
</tr>
<tr>
<td>White</td>
<td>24</td>
<td>21.1</td>
</tr>
<tr>
<td>Yellow</td>
<td>20</td>
<td>25.2</td>
</tr>
<tr>
<td>All</td>
<td>92</td>
<td>22.3</td>
</tr>
</tbody>
</table>

Table 2. Genetic differentiation (\(\Phi_{ST}\)) among years for three populations. Analyses of molecular variation showed no evidence of temporal differentiation within populations (\(P > 0.05\)).

<table>
<thead>
<tr>
<th>Population</th>
<th>(\Phi_{ST})</th>
<th>Years sampled (no. of individuals)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barbados</td>
<td>0.016</td>
<td>2000 (11), 2002 (13)</td>
</tr>
<tr>
<td>Curacao</td>
<td>-0.038</td>
<td>1999 (13), 2002 (13)</td>
</tr>
<tr>
<td>St. Croix</td>
<td>-0.004</td>
<td>2000 (13), 2001 (12), 2002 (15)</td>
</tr>
</tbody>
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References and Notes
Long-Distance Signaling in Nodulation Directed by a CLAVATA1-Like Receptor Kinase

Iain R. Searle, Artem E. Men, Titeki S. Laniya, Diana M. Buzas, Inaki Iturbe-Ormaetxe, Bernard J. Carroll, Peter M. Grishoff

Multicellular organisms need to control the proliferation of pluripotent stem cells, also referred to as meristematic cells in the apices, cambium, and pericycle of flowering plants. Because organ differentiation of plants is predominantly postembryonic and does not involve cell migration, plant stem cells need to be controlled by short- and long-distance signals to achieve equilibrium between cell proliferation and differentiation. The role of short-distance signaling in plant development has been more extensively researched, and some of the key genes involved have been identified (1–8).

Legume nodule formation is an example of a mechanism of development involving long-distance signals. It is initiated by the recognition of rhizobia (a type of bacteria capable of fixing nitrogen) by legume roots. This interaction leads to the formation of nodules, which are specialized structures that allow plants to utilize the nitrogen fixed by the bacteria. The process involves various signaling pathways, including shoot-root signaling, which is critical for the development of the nodules.

The article discusses the role of the CLAVATA1 (CLV1) gene in long-distance signaling in nodulation. Mutations in the CLAV1 gene have been shown to affect nodule development and expansion. The authors present evidence suggesting that the CLAV1 gene is involved in the regulation of legume nodule formation and expansion.

25. We thank L. Taylor, A. Austin, R. Bishop, P. Braulio, K. Cheney, I. Côté, M. Day, S. Macia, O. McMillan, J. Pawlik, M. Robinson, C. Rus, D. Schrier, A. Siemers, C. Thacker, J. Van Tassell, E. Whitman, J. Wilson, R/V Seward John son, R/V Sea Diver, and the Government of the Bahamas for assistance with obtaining specimens; P. Arbour-Reilly, C. Henk, and N. Crochet for technical assistance; and J. Neigel and J. Wares for comments or discussions. Supported by grants from the American Museum of Natural History, the American Society of Ichthyology and Herpetology, and Sigma Xi (Louisiana State University Chapter) to M.S.T. and an NSF grant to M.E.H.

Supporting Online Material

www.sciencemag.org/cgi/content/full/299/5603/107/DC1 Materials and Methods

References

15 October 2002; accepted 22 October 2002