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PERSPECTIVE

Why are marine adaptive radiations rare in Hawai'i?

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Islands can be sites of dynamic evolutionary radiations, and the Hawaiian Islands have certainly given us a bounty of insights into the processes and mechanisms of diversification. Adaptive radiations in silverswords and honeycreepers have inspired a generation of biologists with evidence of rapid diversification that resulted in exceptional levels of ecological and morphological diversity. In this issue of *Molecular Ecology*, tiny waterfall-climbing gobies make a case for their place among Hawaiian evolutionary elite. Moody *et al.* (2015) present an analysis of gene flow and local adaptation in six goby populations on Kaua'i and Hawai'i measured in three consecutive years to try to disentangle the relative role of local adaptation and gene flow in shaping diversity within *Sicyopterus stimpsoni*. Their study shows that strong patterns of local selection result in streams with gobies adapted to local conditions in spite of high rates of gene flow between stream populations and no evidence for significant genetic population structure. These results help us understand how local adaptation and gene flow are balanced in gobies, but these fishes also offer themselves as a model that illustrates why adaptive diversification in Hawai'i's marine fauna is so different from the terrestrial fauna.

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The star of this story is a goby that lives in freshwater streams throughout Hawai'i where in some locations it must scale waterfalls over 100 ft high to reach the upper stretches of streams where adult gobies are able to feed and grow in the absence of aquatic predators. Like all native freshwater fish in Hawai'i, *Sicyopterus stimpsoni* is amphidromous. The adults spawn in streams, but the larvae are washed out to sea where they hatch and spend up to 6 months. Late larval gobies return to river mouths where they settle out as juveniles and make their way upstream. During migrations through the lower reaches of the streams, the juvenile gobies are exposed to aquatic predators before they reach waterfalls and similar barriers. Unlike their predators, the gobies are able to scale waterfalls using a remarkable inchworm-like behaviour in which they alternately stick to the wet rock with an oral sucker and suckerlike pelvic fins (Fig. 1). To inchworm, they extend the head forward while gripping the rock with the pelvic sucker, and then latch on with the oral sucker and pull the tail forward. Once the fish reach the upper regions of a stream, they find a habitat with plenty of algae and detritus to graze and no aquatic predators. Thus, young gobies are exposed to two major threats in the days and weeks after they settle from the ocean to the stream—predation from aquatic predators in the lower reaches of the rivers and waterfalls that must be scaled to escape the predator-rich lower-reach habitat.

The many streams around the coast of each Hawaiian Island vary considerably in the magnitude of obstacles that gobies must scale to reach the adult habitat. In general, streams with steep, terminal waterfalls have short lower reaches, while extended lower reaches can be found in some streams with minimal obstructions to upstream habitats. This topographic variation among streams results in

Fig. 1 Perennial stream on the island of Hawai'i inhabited by the endemic waterfall-climbing goby *Sicyopterus stimpsoni* (left). Age categories and habitat distributions of *S. stimpsoni* (right): juvenile grazing in the estuary of the stream (bottom); adult grazing in the upper reach of the stream (middle); adult male courtship display and breeding coloration in established territory in the upper reach of the stream (top). Image courtesy of K. N. Moody.

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differences in the strength of the two major selective forces during the juvenile stage. Long lower reaches in streams select for better escape performance of juvenile fishes, manifested morphologically in deeper shoulder and caudal regions (Blob *et al*. 2008). Tall waterfalls exert strong directional selection for a more slender body, an enlarged pelvic sucker and a narrower trunk (Blob *et al*. 2010). In the current study Moody and colleagues explored patterns of population differentiation among streams and found that while about 40% of comparisons among juvenile goby subpopulations showed neutral genetic structuring, there was no such structuring in adult stream populations. This pattern in the juveniles is compatible with chaotic genetic patchiness in the larvae arising from temporal and spatial variation in the sources of recruits to streams. However, despite the high gene flow, young juveniles that recently recruited to streams show a pattern of morphological adaptation to local conditions, suggesting some measure of environmental selection in spite of the absence of population structuring in the neutral microsatellite markers.

Waterfall-climbing gobies may seem like a highly specialized fish with little likelihood of offering lessons of general importance, but the biology of this fish, with the tension between local adaptation and high levels of dispersal between adult populations, actually may be typical of marine shoreline fishes. Given that most marine teleosts are shoreline fishes of some sort, either reef fish or soft-bottom animals, these gobies may be giving us a glimpse into very general and widespread aspects of diversification in the sea.

The key life history feature of marine teleosts is that about 99% of them have planktonic larvae that spend a period of days to months in open water before returning to shoreline habitats to metamorphose and settle out as juveniles in the adult habitat. Gene flow between populations is, thus, very high. This is almost certainly the primary reason why there are no honeycreeper-like radiations of marine fishes in Hawai'i. In the sea, reproductive isolation that is sufficient for speciation requires long stretches of ocean or other major barriers that are much larger than the barriers that seem to work in terrestrial habitats on Hawai'i. So, while a quarter of Hawai'i's shoreline fishes are endemics, there are no known cases of marine fish radiations within the Hawaiian archipelago. It seems that local adaptation, even very strong local adaptation like that seen in gobies that must climb waterfalls in one stream and run a gauntlet of predators in another stream, is not sufficient for ecological speciation because gene flow among streams is very high.

It is this contrast between speciation in the sea and in the terrestrial habitats of Hawai'i that the gobies so beautifully illustrate. While the adults live on the islands with the honeycreepers and silverswords, they are tied by their phylogenetic legacy to a reproductive system that enables their tiny larvae to move considerable distances in the ocean. Adaptive radiation on islands can be awesome. Rapid diversification fills a landscape of available niches. But in the sea, it seems to be a different game. There are few examples of empty marine landscapes opening up as happens on islands and in lakes. As a species' range expands in the sea, it is into already heavily occupied territory. And in the ocean, the world is highly connected. Local adaptation of populations might be common, but speciation requires isolation by stretches of ocean that are greater than the distances between Hawaiian Islands. As Moody and colleagues show, diversification in waterfall-climbing gobies is constrained by the same forces faced by the kumu (goatfish), the uhu (parrotfish) and the proverbial humuhumunukunukuapua'a of Kealakekua Bay.

References

Blob RW, Bridges WC, Ptacek MB *et al*. (2008) Morphological selection in and extreme flow environment: body shape and waterfall-climbing success in the Hawaiian stream fish *Sicyopterus stimpsoni*. *Integrative and Comparative Biology*, **48**, 734–749.

Blob RW, Kawano SM, Moody KN *et al*. (2010) Morphological selection and the evaluation of potential tradeoffs between escape from predators and the climbing of waterfalls in the Hawaiian stream goby *Sicyopterus stimpsoni*. *Integrative and Comparative Biology*, **50**, 1185–1199.

Moody KN, Hunter SN, Childress MJ *et al*. (2015) Local adaptation despite high gene flow in the waterfall-climbing Hawaiian goby *Sicyopterus stimpsoni*. *Molecular Ecology*, **24**, 545–563.

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