

NEWS AND VIEWS

PERSPECTIVE

Sympatric speciation without borders?

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The biogeography of speciation remains a controversial issue and the process of allopatric speciation reigns. Sympatric speciation differs from allopatric speciation in terms of geographic setting and the role of selection in bringing about reproductive isolating mechanisms, making it a particularly fascinating and controversial subject for evolutionary biologists. Mayr (1947) explained the difference eloquently: for allopatric speciation, populations spatially diverge and then become reproductively isolated; for sympatric speciation, populations first become reproductively isolated and then diverge. Because of this, sympatric speciation is difficult to show empirically and most evolutionary biologists agree that strict ecological, evolutionary, and geographic criteria must be met (Coyne & Orr 2004). In this issue, Crow *et al.* (2010) challenge us to expand the definition of sympatric speciation by studying species of marine fishes that they propose have arisen by sympatric speciation in a setting that does not appear to conform to the usual geographical criteria.

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When new species arise in sympatry, one has the opportunity to study natural selection while discounting the noise of environmental variation and evolutionary history (Mallet *et al.* 2009). Environmental variation and geography are ingredients that might lead to allopatric speciation but are not drivers of sympatric speciation. Rather than solely its rarity, controversy, and challenges, this is the real attraction of studying sympatric speciation: we can get most purely at the biological forces that lead to diversification.

It continues to be debated what evidence is needed to show that speciation happened under sympatric conditions. Some researchers emphasize that sympatric speciation must occur under conditions of divergence with gene flow while others place primary importance on the geographical setting, i.e. that speciation occurred without spatial barriers to gene flow (Bolnick & Fitzpatrick 2007; Fitzpatrick *et al.* 2008, 2009; Mallet *et al.* 2009). The ‘four

criteria of Coyne & Orr (2004)’ have become the conservative gold standard to establish sympatric speciation: (i) sympatric contemporary distributions; (ii) monophyletic sister taxa not based on hybridization; (iii) substantial reproductive isolation; and (iv) a setting where a history of divergence in allopatry is unlikely. Generally, this has been taken to mean that crater lakes (Barluenga *et al.* 2006; Elmer *et al.* 2009), oceanic islands (Savolainen *et al.* 2006), and other dramatically isolated, homogeneous, and species depauperate locales are the habitats most amenable to sympatric speciation. The most plausible examples of sympatric speciation involve initial ecological divergence followed by the evolution of differential mate choice without spatial isolation, and only a handful of examples pass muster.

In this issue, Crow *et al.* (2010) argue to demote geography as an ingredient of sympatric speciation. Using a creative combination of population genetic, morphological, and *in vitro* methods, the authors focus on mechanistic criteria: the speed and pattern of reproductive isolation developing between sister taxa of fishes in an ocean setting where a history of divergence in allopatry would be entirely likely.

Greenling (Scorpaeniformes: Hexagrammidae) are marine fishes that live in the north Pacific continental shelf. This group of species is renowned for their brilliant colouration, especially in males (Fig. 1). Crow *et al.* (2010) studied three greenling sister species from a genus of six described species: *Hexagrammos agrammus* and *Hexagrammos otakii*, which have overlapping distributions off the east coast of Asia, and *Hexagrammos octogrammus*, which is distributed allopatrically to the east across the Aleutian islands. Sympatric species *H. agrammus* and *H. otakii* differ from each other in size, colour, body shape, meristics, nuptial display, location and timing of breeding, and also



Fig. 1 Male *Hexagrammos otakii* guarding two clutches of eggs. Photo by Ziyusei Kanamoto.

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habitat use (*H. agrammus* inhabits seaweed beds of coastal waters and *H. otakii*, occurs on rocky coastal areas) (Crow *et al.* 2007, 2010 and references therein) (Fig. 2).

The greatest challenge of sympatric speciation is the development of reproductive isolation by natural selection in a group diverging with gene flow (Maynard Smith 1966; Felsenstein 1981; van Doorn *et al.* 2009). In contrast, in allopatric speciation spatial distance itself acts as a prezygotic reproductive barrier and no natural selection is needed since reproductive isolation may evolve in part as a by-product of adaptive differences between isolated populations. Prezygotic isolation can develop quickly by selection in sympatric conditions while postzygotic isolation (e.g. genetic incompatibility) tends to be acquired more slowly. This was first demonstrated empirically by the now famous Coyne & Orr (1989) study of sympatric and allopatric species of *Drosophila*.

Cleverly contrasting this differential rate that reproductive isolation will evolve is one of the most innovative aspects of the Crow *et al.* (2010) study. Theory predicts that if sympatric sister species show pre- but not post-zygotic isolation then they may have speciated by natural selection without geographic isolation. If, on the other hand, species pairs display post- but no pre-zygotic isolation, it suggests that they diverged in allopatry.

The authors use two approaches to assess the strength of these two types of reproductive isolation. First, they screened the morphology and genetics of hundreds of specimens and found no hybrids of the sympatric sister species *H. agrammus* and *H. otakii*. They take this as evidence for prezygotic reproductive isolation in nature. Second, Crow *et al.* (2010) did an experiment that few

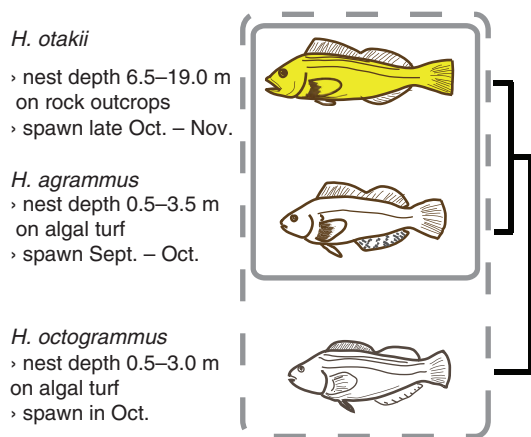


Fig. 2 A schematic summary of some the morphological, ecological, and genetic differences among the three species of greenling. *H. otakii* and *H. agrammus* are found in sympatry (denoted with a solid line) and *H. octogrammus* in allopatry (dashed line). Differences in body length, colouration, number of lateral lines, and caudal fin shape are conveyed in the schematic. Phylogenetic relationships are shown as supported with nuclear and mitochondrial markers. Following Crow *et al.* (2007, 2010).

molecular ecologists studying non-model species even attempt: *in vitro* crosses between all three species to test the strength of genetic, or post-mating, reproductive isolation. They find that the sympatric species *H. agrammus* and *H. otakii* have reduced fertilization success (a post-mating but pre-zygotic test of isolation) but lack post-zygotic reproductive isolation. This fits with expectation for species that diverged without geographic isolation.

The situation for the allopatric species is more complicated. In nature, hybrids are commonly found between the two pairs of allopatric species, but only with *H. octogrammus* as the maternal ancestor and all known hybrids are female (also see Crow *et al.* 2007). *In vitro* experiments generally again mirror the findings from nature (Crow *et al.* 2010). This suggests a complicated sex-linked incompatibility between species and hybrid inviability, which would be a very interesting focus of further research.

Whether all 'required' criteria for sympatric speciation are met with the *Hexagrammos* example is debatable; certainly the geographical one is not. The fact that the sympatric greenling species differ in habitat and peak spawning times may argue for a role of spatio-temporal isolation, so purists who emphasize spatial settings (Mallet *et al.* 2009) over levels of gene flow (Fitzpatrick *et al.* 2008) might not be convinced. Crow *et al.* (2010) contend that the geographical criteria (*sensu* Coyne & Orr 2004) are unnecessary if we are truly interested in evolution and the mechanisms of sympatric speciation, i.e. a role for natural selection rather than geography in reproductive isolation. It remains to be seen how doubters of sympatric speciation will respond to these arguments. Regardless, this study reminds us to think critically about our foundations, definitions, criteria, and goals when we study (sympatric) speciation, be it with or without clear geographic barriers to gene flow.

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