Ecological Speciation in Postglacial Fishes [and Discussion]

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Ecological speciation in postglacial fishes

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SUMMARY

A venerable view of speciation is that reproductive isolation ultimately evolves from contrasting selection pressures between populations exploiting different resource environments. Yet, this 'ecological' mode of species origins has been tested rarely in nature. Here I describe emerging evidence of divergent selection and speciation in fishes of postglacial lakes. Examples of very closely related species pairs within such lakes are known from over a dozen independent fish lineages. These pairs display four remarkable attributes which together raise the possibility of ecological speciation: rapid evolution of assortative mating in sympatry and/or allopatry; persistence in sympatry despite a history of gene flow; a high degree of niche differentiation (usually one species is planktivorous and the other is benthic) accompanied by differences in body size and shape; and high intrinsic viability and fertility of interspecific hybrids. More direct evidence for ecological speciation comes from preliminary confirmation of three predictions: selection against hybrids has an ecological basis (morphologically intermediate hybrid sticklebacks have a reduced ability to exploit the main resources on which the parent species are specialized); premating isolation is linked to the morphological traits that have diverged between species (hybridization in sticklebacks occurs only between the morphologically most similar individuals of the two parent species); premating isolation mechanisms evolve in parallel in similar environments (interspecific mate preferences appear to have diverged in parallel in stickleback species pairs that evolved independently). These findings argue that knowledge of ecological environments is essential to understanding the origin of species in adaptive radiation, and perhaps more generally. Field studies of selection on traits determining reproductive isolation are sorely needed, and would complement (and perhaps transform) traditional genetic approaches to speciation.

1. THEORIES OF ECOLOGICAL AND NON-ECOLOGICAL SPECIATION

The ecological processes that drive speciation are poorly understood. The topic has received only sporadic attention over the past few decades, confined largely to a fraction of literature devoted to the possibility of speciation in sympatry (Rice & Hostert 1993; Bush 1994). But progress in identifying environmental mechanisms has been slow regardless of the putative geographic mode of speciation. By 'speciation' I mean the evolution of reproductive isolation. 'Ecological processes' are the interactions between individual organisms and their environment that cause natural selection and that drive population establishment, growth and decline.

This gap in our understanding is most glaring in the context of adaptive radiation in novel environments, such as remote archipelagoes and newly formed lakes. Rates of species accumulation are often accelerated in such circumstances, and speciation is typically accompanied by substantial shifts in phenotype (morphology, physiology, and resource use). Phenotypic differentiation in adaptive radiation is probably the outcome of strong natural selection (Lack 1947; Simpson 1953; Schluter & Grant 1984; Grant 1986; Schluter 1988, 1994), but what drives speciation?

Perhaps the oldest hypothesis for the origin of biological species (Mayr 1942) is that reproductive isolation evolves ultimately from the same forces that cause phenotypic change: divergent selection stemming from the exploitation of alternative resource environments and from resource competition. For example, Dobzhansky (1951) believed that 'the genotype of a species is an integrated system adapted to the ecological niche in which a species lives. Gene recombination in the offspring of species hybrids may lead to discordant gene patterns.' I will use 'ecological speciation' to refer to the process whereby reproductive isolation evolves from divergent selection, to emphasize the vital contribution of resource environment. 'Non-ecological' modes of speciation are those in which reproductive isolation evolves by genetic drift, founder events, or fixation of alternative advantageous alleles in separate populations experiencing the same natural selection pressures (cf. Barton 1989). Despite reasonable arguments and experimental models for ecological speciation (Barton 1989; Rice & Hostert 1993; Coyne 1994), I am not aware of a single study that successfully links the evolution of reproductive isolation in nature to niche-based divergent natural selection.

In this report I show how recent studies of fish in postglacial lakes are beginning to provide these links. I begin with a summary of island-like properties of post-

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glacial lakes from the perspective of the fish inhabiting them. I then review examples of rapid fish speciation in postglacial lakes and their common features. Finally, I summarize tests of ecological speciation in these fishes. Throughout, I focus on the broad issue of ecological speciation rather than on the subsidiary questions of whether it took place in allopatry or sympatry, and whether premating reproductive isolation evolved solely as an incidental by-product of divergent selection or additionally required reinforcement.

2. FISH SPECIATION IN POSTGLACIAL LAKES

(a) Recent lakes as islands

Most of the vast numbers of lakes scattered over the northern parts of North America and Eurasia were formed after the immense sheets of ice that covered the region retreated about 15 000 years ago (e.g. see maps in Harrison 1982 and Pielou 1992). The lakes were subsequently colonized by fish from glacial refugia, a process that was impeded by the limited number and duration of passage routes. Marine access to coastal lakes and rivers was limited to salt-tolerant species, and changes in sea level meant that many lakes were accessible for only a short period (McPhail & Lindsey 1986). Species intolerant of salt water dispersed inland via infrequent changes in the drainage patterns of lakes and rivers during deglaciation (McPhail & Lindsey 1986). Lakes and watersheds of previously glaciated areas are therefore like islands in important ways: movement between them was sporadic, their faunas are depauperate and heterogeneous, and separate drainages constitute evolutionarily independent units.

Fish species pairs in recently glaciated lakes share four remarkable attributes that together implicate ecological selection in the speciation process: rapid evolution of reproductive isolation, persistence (and perhaps origin) in the face of gene flow, a high degree of niche differentiation, and high intrinsic viability and fertility of hybrids. I summarize each of these elements in turn.

(b) Rapid evolution of reproductive isolation

Elevated rates of speciation are indicated by the variety of cases in which two very closely related species coexist in lakes less than 15 000 years old. The examples in table 1 are the subset of cases for which genetic distances (Nei's D or equivalent) are small but significant $(0 < D \leqslant 0.06)$, independent evidence of assortative mating exists (indicated by a paucity of morphological hybrids, separate breeding times or localities, and/or mating observations), and evidence suggests that morphological differences are genetic rather than environmentally induced. Not yet added to the table are cases in which evidence on genetic differences are still uncertain or lacking; these include omul in Lake Baikal (*Coregonus autumnalis*; Smirnov et al. 1992), cisco in Quebec (*Leucichthys artedii*; Henault & Fortin 1989), European whitefish (*C. lavaretus*) and vendace (*L. albula*) in Scandanavia (Svardson 1979),

kokanee salmon in Kamchatka (*Oncorhynchus nerka kennerlyi*; Kurkenov 1977) and pygmy whitefish in Alaska (*Prosopium coulteri*; McCart 1970).

These examples include a diversity of fish taxa, although salmonids (salmon, trout, whitefishes) predominate. In all instances both species retain the same latin binomial, underscoring the confusion surrounding their taxonomic status. I am unaware of an equivalently large set of examples from fish in unglaciated regions of the temperate zone. Low levels of interspecific genetic divergence are occasionally seen there, such as in the desert pupfishes of the American Southwest (Soltz & Hirshfield 1981), but the most closely related species are not as often sympatric.

(c) Gene flow and species origins

Phylogenetic studies suggest that rates of both allopatric and sympatric/parapatric speciation are elevated. Lake whitefishes of eastern Canada and Maine offer the clearest case of a species pair that resulted from separate invasions by previously allopatric ancestors. Sympatric 'dwarf' and 'normal' whitefishes in one lake are fixed for alternative mtDNA haplotype groups whose main geographical distributions lie to the southwest and northeast, respectively, in association with different late-Pleistocene refugia (Bernatchez & Dodson 1990). The situation is less clear-cut in nearby lakes. Both haplotype groups occur in one of two species in a second lake, suggesting mtDNA gene flow after secondary contact. Both mtDNA groups are also present in the sole species present in a third lake, hinting it is a collapsed species pair.

Sockeye salmon represent the most likely case of sympatric or parapatric speciation. Anadromous sockeye salmon spend the first year or two of their life in large lakes before migrating to sea where they attain a large size. Kokanee salmon reside permanently in lakes and grow to a much smaller size. The two forms overlap in breeding season and localities yet are genetically distinct. Phylogenies based on allozymes, minisatellite DNA, and mtDNA all show that kokanee are polyphyletic and arose independently several times from anadromous sockeye within different river systems (Taylor et al. 1996a). This conclusion is bolstered by the spontaneous appearance of a small-bodied, freshwater resident salmon in river systems outside the natural range of sockeye after artificial transplants of only the anadromous form (Taylor et al. 1996a).

Geographic modes of speciation for most other cases are less certain, even with molecular surveys. Genetic data for several are consistent with sympatric speciation but can also be explained by double colonization whose trace was obscured by subsequent gene flow. Lake whitefish of Yukon and Alaska (table 1) highlight the difficulty of distinguishing these modes. Two mtDNA haplotype groups are present, one of which (II) is found exclusively in or near remnants of former Beringia whereas the other (III) is chiefly Eurasian (Bernatchez et al. 1996). In Little Teslin Lake in the Yukon River system the limnetic whitefish species is mainly group II whereas the benthic is fixed for group

Table 1. *A selection of examples of recent sympatric species pairs in lakes and rivers of recently glaciated areas*

(Genetic differences are in the format $x/y/z$ where x is Nei's distance based on electrophoresis; y is mtDNA sequence divergence estimated using restriction enzymes; z is % mtDNA 'nucleotide divergence' (Nei & Miller 1990), which combines differences in both nucleotide sequence and haplotype frequency.)

nominal species	region	trophic characteristics	genetic difference
Threespine stickleback[a] *Gasterosteus aculeatus*	British Columbia	limnetic (planktivore) benthic (benthivore)	0.02/–/0.10
Lake whitefish[b] *Coregonus clupeaformis*	E. Canada, Maine	dwarf (planktivore) normal (benthivore)	0.01/0.5/–
Lake whitefish[c] *C. clupeaformis*	Yukon, Alaska	high gill rakers (planktivore) low gill rakers (benthivore)	$0.01-0.02/-/\leqslant 0.30$
Sockeye salmon[d] *Oncorhynchus nerka*	W. Canada, Alaska	sockeye (anadromous) kokanee (freshwater resident)	$\leqslant 0.02/-/-$
Atlantic salmon[e] *Salmo salar*	Newfoundland	anadromous freshwater resident	0.06/–/–
Brown trout[f] *Salmo trutta*	Ireland	sonaghen (planktivore) gilaroo (benthivore)	0.04/–/–
Brown trout[g] *S. trutta*	Sweden	planktivore benthivore	0.03/–/–
Arctic charr[h] *Salvelinus alpinus*	Scotland	planktivore benthivore	$\leqslant 0.02/-/-$
Arctic charr[i] *S. alpinus*	Iceland	planktivore & piscivore small & large benthivore	$\leqslant 0.001/-/\leqslant 0.01$
Rainbow smelt[j] *Osmerus mordax*	E. Canada, Maine	dwarf (planktivore) normal (benthivore, piscivore)	$-/-/0.01-0.10$

[a] Enos and Paxton Lakes. McPhail (1992), Schluter & McPhail (1992), Taylor *et al.* (1996*a*).

[b] Fenderson (1964), Kirkpatrick & Selander (1979), Bernatchez & Dodson (1990).

[c] Bodaly (1979), Bodaly *et al.* (1992), Bernatchez *et al.* (1996).

[d] Ricker (1940), Foote *et al.* (1989), Taylor *et al.* (1996*b*).

[e] Verspoor & Cole (1989), Claytor & Verspoor (1991).

[f] Lough Melvin. Ferguson & Taggart (1991), McVeigh & Ferguson (1988). A third piscivorous species (ferox), somewhat more distantly related to the other two (Nei's $D = 0.08$) is also present.

[g] Lake Bunnersjöarna. Ryman *et al.* (1979), N. Ryman (personal communication).

[h] Loch Rannoch. Gardner *et al.* (1988), Walker *et al.* (1988), Hartley *et al.* (1992).

[i] Lake Thingvallavatn. Magnusson & Ferguson (1987), Danzmann *et al.* (1991), Malmquist *et al.* (1992), Skúlason *et al.* (1992), Snorrason *et al.* (1994). Four trophic forms are present, and their relationships and species status are still unclear. However, preliminary indications are that two genetically distinct lineages are present, each of which has two developmental morphs, as listed above (Skúlason *et al.* 1992).

[j] Taylor & Bentzen (1993).

III, supporting an allopatric origin of species with scant gene flow after secondary contact. But in Squanga Lake, a few kilometres upriver, a single group III haplotype predominates in both species; in Dezadeash Lake in the Alsek River system (which was temporarily joined to the Yukon during deglaciation), the limnetic and benthic species are fixed for (different) group III haplotypes. Gene flow has evidently occurred between forms within lakes, but additional data are needed to determine whether it occurred before sympatric speciation within each lake or after double invasion. Allozyme frequencies support the former interpretation – they are virtually identical between sympatric species in all three lakes – but this too could have resulted from gene flow after secondary contact (Bernatchez *et al.* 1996).

The origin of limnetic-benthic pairs of threespine sticklebacks in British Columbia (table 1) is similarly obscure. A phylogeny based on mtDNA restriction fragments suggests that each pair originated independently by sympatric speciation (Taylor *et al.* 1996*b*). However, the result contradicts earlier evidence that the limnetic species in each two-species lake is more similar to the modern marine species of

stickleback in allozyme frequencies and in salinity tolerance of embryos than is the second (McPhail 1992; Kassen *et al.* 1996), a pattern more consistent with double invasion from the sea.

Two conclusions may be drawn from the genetic data despite uncertainty over origins. First, most sympatric species pairs have persisted in the face of gene flow. Whether gene flow diminished gradually in sympatry from initially high levels (sympatric speciation) or was only moderate to begin with (double invasion) remains to be determined. In either case selection against intermediate phenotypes is implicated, else premating isolation would have decayed through time. Second, even if most sympatric species pairs were formed out of previously allopatric populations, the small genetic differences between alternative mtDNA lineages in most cases ($< 0.5\%$ sequence divergence; Bernatchez & Dodson 1990; Bernatchez *et al.* 1996; Taylor *et al.* 1996*a, b*) ensures that the period of allopatry could not have been prolonged.

(d) Ecological and morphological differentiation

A large degree of ecological differentiation is a consistent feature of sympatric species pairs. Most remarkable are the repeated instances of divergence along similar ecological gradients (Schluter & McPhail 1993; Robinson & Wilson 1994). In the majority of cases one of the species is pelagic and specializes on zooplankton whereas the other is more benthic, consuming larger invertebrates obtained from sediments or on plants in more littoral habitats (table 1). A consistent set of morphological differences is associated with this habitat split: planktivores are smaller and more slender than benthivores and tend to have narrower mouths and longer, more numerous gill rakers. (Gill rakers are protuberances along the gill arches that seive ingested prey or direct water currents and particle movement within the buccal cavity; Sanderson *et al.* 1991.) Such differences are arguably important only because they lower incidence of competitive exclusion. However, ecological and morphological differentiation may reflect divergent selection pressures between resource environments, the basis of ecological speciation.

Evidence for divergent selection between limnetic and benthic habitats is threefold. First, morphological divergence has rendered the species differently capable of exploiting these two habitats (Malmquist 1992; Schluter 1993; see also Robinson *et al.* 1996). In open water (presented in large aquaria with natural prey densities) limnetic sticklebacks captured plankton at three times the rate achieved by benthics, an advantage that was reversed in the littoral zone. Second, growth rates measured in a transplant experiment in the wild mirrored results on foraging efficiency: limnetic sticklebacks grew at double the rate of benthics in open water; benthics held an equivalent advantage in the littoral zone (Schluter 1995). Third, observations and experiments suggest that ecological and morphological divergence in sympatry is greater now than in the past and was driven by competition for food. Stickleback species occurring alone in small lakes ('solitary') are morphologically intermediate between limnetics and benthics and exploit both habitats (Schluter & McPhail 1992). In a pond experiment natural selection favoured the more benthic-like individuals within a solitary species after introduction of a planktivore (Schluter 1994).

These examples refer only to foraging habitats; differences in breeding habitats also exist but are often less. For example, both sticklebacks breed in close proximity in the littoral zone, albeit in different microhabitats (Hatfield 1995). Anadromous salmon return from the ocean to breed in many of the streams in which kokanee also spawn (Ricker 1940). This dissociation between feeding and breeding contrasts with many specialized insects for which divergence onto a new host yields habitat-based assortative mating as a by-product (Bush 1994). In postglacial fishes the link between divergent selection on foraging niche and the evolution of habitat-based premating isolation seems less straightforward. Species pairs usually differ in time and location of spawning, and possibly this evolved independently of foraging habitats and for different selective reasons. Or, divergence in feeding niche may have led to separation in breeding habitat and time by one of three mechanisms: genetic hitch-hiking, altered ensuing selection pressures on life history, and reinforcement of premating isolation. Finally, it is conceivable that divergent selection on breeding habitat and time in some instances facilitated subsequent divergence in foraging niche. The existence of genetically different stocks of salmon that do not overlap in breeding time but exhibit little or no ecological differentiation (Tallman & Healey 1994) lend credence to the last possibility.

(e) High viability and fertility of hybrids

Finally, study of a small but growing number of species pairs indicate that intrinsic viability and fertility of interspecific hybrids is high. Laboratory growth rates of F_1 and F_2 hybrids between limnetic and benthic sticklebacks are simply the average of that of their parents; growth of backcrosses is only slightly lower (Hatfield 1995). F_1 hybrids between sockeye salmon and kokanee are highly viable in a laboratory setting (Wood & Foote 1990). Hybrid breakdown arising from incompatability of species genomes is therefore not the basis of postmating isolation between these young species. Instead, it is likely that hybrid inferiority has an ecological basis, a possibility discussed in the next section.

3. TESTS OF ECOLOGICAL SPECIATION

The above patterns, although suggestive, beg for more direct tests of ecological speciation. Unfortunately, progress in this regard has been limited. Here I summarize preliminary tests of three predictions.

(a) Ecological basis of postmating isolation

The first expectation is that selection against hybrids should have an ecological basis. This prediction stems from the observation that postmating isolation in the lab is virtually lacking, yet hybrids have an intermediate phenotype that is expected to compromise their efficiency of resource exploitation. The prediction was tested using lab-raised limnetic, benthic and F_1 hybrid sticklebacks by transplanting individuals to enclosures in the lake and recording growth rate (Hatfield 1995). The hybrids grew more slowly than benthics in the littoral zone and more slowly than the limnetics in open water, supporting the expectation. Their growth deficiency matched observations of reduced food consumption rates in both habitats: hybrids are less successful at capturing plankton than limnetics and consume smaller prey in the littoral zone than benthics (Schluter 1993).

Less information is available from other systems, as hybrid transplants to the wild have not been attempted. However, hybrids between sockeye salmon and kokanee are intermediate in saltwater capability, and their larvae hatch earlier or later than larvae of the parent species, depending on the identity of the

maternal and paternal parents (Wood & Foote 1990). Presumably, selection for different saltwater capabilities and synchronous hatching times between ocean-going and freshwater resident salmon acts against hybrids in the wild, but the crucial experiments have not yet been done.

(b) Morphology-based assortative mating

Under the hypothesis of ecological speciation, premating isolation also evolves as a consequence of divergent selection between resource environments. But this may happen via many routes: mating preferences may diverge because natural selection directly favours it; because the preferences are correlated genetically with phenotypic traits under divergent selection; or for other reasons, which means that a general procedure won't suffice to test all cases. In postglacial fishes, two kinds of tests have been attempted. The first examines whether mating preferences are dependent on the very phenotypic traits that have diverged between species. The second, summarized in the next section, asks whether the same premating isolating mechanism have evolved in parallel multiple times under similar environmental selection pressures.

At least two studies have confirmed that morphological traits determining feeding efficiency, especially body size, also strongly influence the probability of mating. In laboratory mating experiments in sticklebacks, heterospecific matings took place only between the largest females of the smaller species (limnetics) and the smallest males of the larger species (benthics); and between the largest limnetic males and smallest benthic females (Schluter & Nagel 1995). Assortative mating in sockeye salmon is based on the large differences in body size between the anadromous and freshwater resident forms (Foote & Larkin 1988). Finally, male F_1 hybrid sticklebacks are less preferred as mates by limnetic and benthic females, possibly because they are morphologically intermediate (Hatfield 1995).

(c) Parallel speciation

Finally, mechanisms of premating isolation between species may have evolved in parallel independently in different lakes, under similar ecological conditions. I call this phenomenon 'parallel speciation' and argue that it is strong evidence for natural selection, for the same reason that other forms of parallel evolution are evidence for adaptation: drift is unlikely to produce repetitive shifts in the same direction under a specific environmental setting (Schluter & Nagel 1995). As an example scenario for parallel speciation, consider an ancestral species which independently gives rise to multiple new populations at the periphery of its range in two different types of environment. Parallel speciation by natural selection occurs when reproductive isolation evolves between descendant forms adapting to different environments, but not between descendants adapting to similar environments.

Indirect evidence that parallel speciation has occurred is that mate choice is often based on body size, and that divergence in size has occurred independently on multiple occasions (Schluter & Nagel 1995). For example kokanee salmon, which are small in size, have evolved repeatedly from large-bodied anadromous sockeye. If size is a major determinant of assortative mating (Foote & Larkin 1988) then separate, independently derived kokanee populations should not be reproductively isolated from one another. The crucial test of assortative mating between kokanee populations remains to be done.

A second apparent case of parallel speciation occurs in the sticklebacks, where limnetics and benthics have apparently evolved independently on multiple occasions (Schluter & McPhail 1992; Taylor *et al.* 1996*b*), and where assortative mating is also size-based (Schluter & Nagel 1995). Nagel (1994) showed that assortative mating between limnetics from different lakes (Paxton and Priest Lakes, Texada Island, British Columbia) was weak, and also that there was no detectable assortative mating between benthics from these same two lakes nor between them and Benthics from Enos Lake, Vancouver Island, British Columbia. In other words, fish of similar body size and shape that exploit similar ecological environments have similar mate preferences. These results are still tentative evidence for parallel speciation because the phylogenetic relationships among these species is still uncertain (Taylor *et al.* 1996*b*).

4. DISCUSSION

In the first half of this century, the idea was developed that divergent natural selection may cause reproductive isolation to evolve between populations exploiting different resource environments. Yet evidence from nature remains scarce in some measure because few have tested it. This lack of progress is partly the result of a historical preoccupation with other issues, especially the geographic mode of speciation (sympatric versus allopatric) and the contributions of 'genetic' mechanisms other than selection i.e. drift and founder events. Establishment of the principle that speciation is chiefly allopatric might even have discouraged the study of natural selection in speciation. Random drift and other non-ecological mechanisms inevitably cause sterility and inviability in crosses between populations geographically isolated for a sufficiently long time; ecological processes are not therefore needed to explain the fact of species. However, divergent selection can cause reproductive isolation much sooner than drift, and may allow stable sympatry after a period of geographic isolation too brief for drift to effect much change.

This report summarizes the contributions that studies of fish in postglacial lakes have made to the question of speciation by divergent selection. Postglacial lakes contain a wealth of examples of coexisting species exhibiting marked levels of ecological and morphological differentiation despite low levels of genetic divergence. Phenotypic differences in sympatry

are primarily the outcome of markedly different selection pressures in alternative lake habitats, and by competition for food. Gene flow, either before sympatric divergence or after secondary contact between previously separated lineages, was habitual but did not prevent speciation. Nor did gene flow cause species pairs, once created, to collapse to hybrid 'swarms' despite high fertility and viability of hybrids. Hybrid fitness is strongly environment-specific, and appears to stem directly from the disadvantage of having an intermediate phenotype. Mate choice is based in part on morphology, and hence premating isolation evolved in concert with morphological differentiation. Premating isolation may have evolved in parallel in independent populations experiencing similar selection pressures.

Much of these data are preliminary and await detailed confirmation. In addition, much more effort is necessary to clarify the mechanisms of selection and the precise basis of pre- and postmating isolation. Nevertheless the results strongly point to ecological selection pressures as the primary cause of rapid speciation in these fishes. At this point, it is difficult to conceive of alternative non-ecological modes of speciation that would account for such a consistent set of findings. The context of these results is the depauperate lake environment; hence these findings give insights into the causes of speciation especially during adaptive radiation in novel environments.

At the very least these results demand a reappraisal of the role of ecology in speciation, and for a renewed effort to understand mechanisms of selection leading to the evolution of reproductive isolation. There has been a tendency in recent years for researchers to infer mechanisms of speciation in nature entirely from genetic measurements, particularly the genetic basis of reproductive isolation and the deduced strength of selection acting on hybrids. Such evidence is undeniably crucial, but will of itself lead to a poor understanding of the causes of speciation. A complementary natural history of the evolution of reproductive isolation is needed in addition. In the same way that field studies of selection on beak size and shape have revealed much about the causes of morphological diversity, so too might field studies of selection on traits conferring degrees of reproductive isolation reveal much about the ecological causes of speciation.

Indeed, such field studies might change the questions we ask in genetic studies of speciation. For example, laboratory measures of hybrid sterility and inviability (Dobzhansky's 'discordant gene patterns') are standard traits for dissecting the genetic basis of postmating isolation. Yet, such measures may evolve comparatively slowly, if the high fertility and viability of hybrid postglacial fishes is any guide; indeed they may often evolve after speciation is already complete. It makes sense to focus genetic studies instead on earlier stages of ecological speciation. For example, when viability of hybrids is determined by the efficiency with which they can exploit environmental resources, or when mating success of hybrids is determined by degree of resemblance to the parent species, the most interesting genes

– those underlying postmating isolation – are those that cause hybrids to be phenotypically intermediate. Because of their tractability for ecological experiments and the simplicity of their environments, studies of postglacial fishes can contribute much to a joint endeavour.

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Discussion

ANDREW RAMBAUT (*Department Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.*) You showed that the F_1 hybrids of the benthic and limnetic forms showed reduced ecological fitness due to their intermediate morphology. How do you reconcile this with the fact that most solitary species exist in such an intermediate form?

D. SCHLUTER. I would like to know more about what is happening in the solitary species, which in small lakes are intermediate and tend to exploit both habitats (littoral invertebrates and open water plankton). One explanation is that solitary species are held at an intermediate position by frequency-dependent disruptive selection. For example, an increase in the frequency of the more planktivorous phenotypes within the species would cause a decline in the abundance of plankton. Selection would then favour the more benthic phenotypes at the other extreme of the phenotype distribution, because their resources are less depleted, and pull the species mean phenotype back to an intermediate position. Without assortative mating between like individuals at the extremes, an intermediate phenotype could perhaps be maintained indefinitely. The second possibility is that selection is stabilizing when only a single species is present in a lake, and favours an intermediate phenotype. Peaks in resource abundance in the two habitats typically occur at different times of the year: spring in the littoral zone, and summer in the open water. In the absence of high densities of phenotpyes specialized for these two habitats (i.e. limnetics and benthics) an intermediate generalist may be able to take advantage of both resources in alternation. Future work will attempt to distinguish between these possibilities. The issue is crucial, as only the first scenario (disruptive selection) would be conducive to sympatric speciation. If the second scenario prevails, then evolution of a species pairn would require a double invasion.