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Charr truth: sympatric differentiation in *Salvelinus* species

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Abstract Charrs, *Salvelinus* species, are characteristic fishes of northern freshwater lakes and rivers. They are highly variable in almost every aspect of their behaviour, morphology and life history. Several possible explanations have been proposed to account for this variability and resolve the taxonomic confusion in this genus. I propose that sympatric trophic polymorphism, in the ecological context of these species, can make sense of this variability. I use examples from charr in Canada and Iceland to construct an evolutionary scenario for this genus.

Keywords *Salvelinus* species · Resource polymorphism · Sympatric speciation · Evolution · Behavior

Introduction

A great deal of attention continues to be directed to the question of sympatric speciation, after an extended period of time when the subject was almost universally dismissed. Mayr (1963) gave perhaps the most detailed and forceful rejection of sympatric speciation as either a theoretical or empirical possibility. Since then the concept has been revisited and a number of credible theoretical models (e.g., Maynard Smith 1966; Wimberger 1994; Foster et al. 1998; Dieckmann and Doebeli 1999; Bolnick 2004) and empirical examples (e.g., Taylor and McPhail 1985; Swain and Holtby 1989; Schluter 1994, 1995; Dynes et al. 1999; Wilson 1999) have been published. I will not review those studies nor do I intend to test any of those models with experimental data. Rather I will summarize my comparative approach and present a model to stress the importance of sympatric process rather than pattern in the evolution of *Salvelinus* species. The interesting matter is not how many species there might be, but how those species arise.

Charrs are enigmatic fishes. They have long plagued taxonomists as the "charr problem" because of the high degree of variability within species (Kawanabe et al. 1989). They are the focus of the continuing series of international charr conferences (Johnson and Burns 1984; Kawanabe et al. 1989; Magnan et al. 2002). They are important as food for aboriginal peoples (Power 2002), as the favoured species of recreational anglers (Curry et al. 1995, 1997), and as indicators of environmental quality (Gunn and Noakes 1987; Gunn et al. 1987). They are native to north temperate and arctic environments (Gunn and Keller 1985), most are landlocked but some are anadromous (Kawanabe et al. 1989). The two features that initially attracted me to them as research subjects were the high degree of variability within and between species (Fig. 1), combined with the virtually unlimited fertility of artificially produced

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Fig. 1 Four sympatric morphs of arctic charr, *Salvelinus alpinus*, from Thingvallavatn, Iceland. From *top to bottom* they are: piscivore, small benthivore, planktivore and large benthivore. All these fish were caught in the same set of one gill net during the evening of 1 July 2003 (photograph by David Noakes)

crosses between different species (Noakes 1986, 1989).

Salmonids have commonly been used in studies of physiology, endocrinology, ecology, nutrition and genetics (e.g., Brett 1965; Beamish 1978; Carl and Healey 1984; Ferguson 1986; Leatherland 1994) so there is a wealth of data available on these aspects of their biology. There is also a long history of laboratory and field studies on salmonids as their native ranges coincide with the north temperate distribution of universities, research institutions and management agencies (Scott and Crossman 1973; Magnan at el. 2002). Populations of many species are readily accessible for studies within their native habitats (Magnan 1988). Many species attract significant research support as a consequence of their economic importance to aboriginal, recreational or commercial harvest.

My research interests have always been in development and social behaviour (Noakes 1978a, b, c). My initial choice of charrs as study species was motivated by all these considerations, plus some added features of three key species available to me. Brook, *S. fontinalis*, lake, *S. namaycush*, and arctic, *S. alpinus*, charr differ strikingly in their native habitats, biology and behaviour (Noakes 1989, 1994; Noakes et al. 1989). However, they are all characterized by a number of features that I believe are important for their evolution. They are native to northern lakes & rivers, including many that have been recently deglaciated, on a geological time scale. They are native to areas with few species, particularly few competitor species. They appear to be suited as recent invaders to habitats created by melting of glaciers (Fig. 2). As mentioned, they are known to be highly

Fig. 2 Melting water from a glacier in Iceland running off through rocks, sand and gravel deposited by the melting glacier to form a glacial river (photograph by David Noakes)

variable species, but the basis for that variability has seldom gone beyond speculation and description of the various morphs, or forms, or subspecies encountered (Frost and Kipling 1980; Partington and Mills 1988). Certainly one possibility is that these fishes are examples of pure phenotypic plasticity. I will argue that a more likely hypothesis to account for their variability is resource polymorphism (Fig. 1).

The Ontario Ministry of Natural Resources conducted a management program with hybrids between brook and lake charr for a number of years (Berst and Spangler 1970; Berst et al. 1980; 1981). That program regularly produced large numbers of hybrids, and backcrosses up to the F-9 backcross generation. We utilized those in a productive series of studies of behavior genetics (Ferguson and Noakes 1981, 1983a, b, c). Our studies showed a significant genetic basis for the behavioral differences between these species. Those and subsequent studies of these species elaborated on the adaptive nature of the behavior of the species, including the differences between the species in their responses to environmental factors (Ferguson et al. 1983; McNicol and Noakes 1984; Noakes and Grant 1986, 1992; Noakes and Curry 1995; Biro et al. 1997).

The foraging and social behavior of juvenile brook charr is particularly interesting and we have devoted considerable study to the details of that system (Grant and Noakes 1986, 1987a, b, c, 1988; Grant et al. 1989; Imre et al. 2001; McLaughlin 2001; McLaughlin and Grant 1994, 2001; McLaughlin et al. 1992, 1994; 1995a, b, 1999, 2000; McLaughlin and Noakes 1998). The important conclusion that I want to note from these studies is that young brook charr in streams tend to behave in one of two alternate tactics. We labeled those as “movers” or “stayers”, respectively. Individual fish behaving as movers show low levels of agonistic behavior. They move relatively frequently and forage mostly on prey taken from the water surface or on the substrate. Individual fish behaving as stayers move much less frequently. They show high levels of agonistic behavior and forage primarily on prey carried to them as drift by the water current (Noakes 1994). A good deal of earlier literature of the behavior of juvenile salmonids in streams had described similar differences in behavior and had assumed that stayers represented the only successful tactic. Movers were generally assumed to be making the best of a bad lot, as a consequence of their smaller size, failure to obtain or hold a territory or late emergence from the redd after all suitable territories had been taken (Noakes 1978a). Detailed studies of foraging activities, growth rates and social interactions of these juvenile brook charr clearly showed that this is not the case. We used a combination of observations and measurements of behavior and growth in both the field and the laboratory to compare growth rates of individual fish showing a range of social and foraging activities. Juvenile stream salmonids must grow rapidly and accumulate somatic energy resources or they will not survive their first winter (McNicol and Noakes 1981, 1984). The fitness payoffs of the behavioral tactics are such that movers and stayers have comparable high fitness, as estimated by growth rate (McLaughlin et al 1999). Individual fish showing other behavioral tactics, or some combination of moving and staying, have significantly lower growth rates, and hence lower fitness.

Furthermore, there is a significant correlation between these behavioral tactics and morphology of the young brook charr, and the microhabitats characteristic for the individuals (McLaughlin et al 1992; McLaughlin and Grant 1994; McLaughlin 2001). Stayers tend to hold position in faster water current and they have significantly narrower caudal peduncles and larger caudal fins. Both of these features are associated with higher swimming efficiency in fast water current (Brett 1965). Young brook charr reared in faster water currents develop some of these morphological differences (Imre et al. 2002), showing that at least of the differences are the result of phenotypic plasticity. We have used this evidence as an important part of the more general hypothesis of evolution within the genus, as I will elaborate below.

Our concurrent studies of the details of social and foraging behavior in juvenile lake charr showed a striking contrast to the situation with juvenile brook char. In general, juvenile lake charr behave as movers. They rarely show any agonistic behavior, they move frequently and they forage opportunistically on prey they encounter during their movements. All individuals are consistent in their social and foraging behavior, and variations in water current velocity have no significant effect on social or foraging behavior (Ferguson et al. 1983). There is a strong genetic basis for the differences in species–typical behavior (Ferguson and Noakes 1981), including a significant maternal effect on inheritance (Ferguson and Noakes 1983a). The differences between the species correspond to the typical habitats of these species (Noakes 1989), juvenile brook charr most commonly live in the flowing waters of streams and juvenile lake charr most commonly live in the lentic waters of lakes. We can understand the behavior of these two species as a consequence of the adaptive nature of the species–typical behavior, including the degree of plasticity of that behavior in response to environmental variability. The most important environmental factor is water current, both directly as a physical factor and indirectly through its effects on spatial and temporal predictability of food supply for the fish. The predictable, directional flow of water in streams ensures that potential food items will be delivered predictably in time and space as drift from the upstream direction, and is an increasing function of current velocity. Consequently a central place foraging territory becomes increasingly profitable (net benefit increases), given limitations of competitor density and extreme water current velocity (Grant and Noakes 1987c). Juvenile brook charr respond adaptively to water current velocity, the faster the current the more likely the fish will behave as stayers. Juvenile brook charr exposed to low water current velocity are more likely to behave as movers, since the net benefit (food delivered as drift by the water current) from the territory decreases. In contrast, juvenile lake charr do not show any consistent change in behavior across the same range of water current velocities (Ferguson et al. 1983). Juvenile charr in lakes will rarely if ever encounter the consistent, directional water current found in streams, so there is no advantage to defend a fixed, central place foraging territory, or to evolve plasticity in their response to water current velocity (Noakes 1989). In contrast, juvenile brook charr will certainly encounter a range of water current velocities in streams, so it is not surprising that they show plasticity in their response to water current.

Interestingly, the behavior of juvenile brook charr in lakes confirms the generality of these findings. Juvenile brook charr in lakes, where directional water currents do not exist, behave as movers (Biro et al. 1997). They behave essentially as juvenile lake charr would in that situation. Thus we concluded that the species–typical behavior of each species, including the plasticity of that behavior, can be understood as adaptive to the characteristic habitat of the species.

We extended this background to the behavior and ecology of Arctic char, through our studies of that species in Iceland (Skulason et al. 1996). This species, particularly in Iceland, epitomizes the “charr problem” in terms of the bewildering range of variability in morphology, behavior, life history and ecology (Fig. 1). We demonstrated that those differences are genetically based (Perrault et al. 1990; Skulason et al. 1989a, b, 1993, 1996, 1999; Snorrason et al. 1994). Individuals produced by artificial crosses between adults of different morphs develop intermediate phenotypes in common garden experiments (Skulason et al. 1996; Eiríksson et al. 1999). The genetic differences between sympatric morphs are small (Danzmann et al. 1991; Ferguson et al. 1990; Noakes et al. 1989) but they correspond well with ecological and morphological differences (Gislason et al. 1999). Furthermore, and most importantly, it is clear that these differences have arisen sympatrically, almost certainly as a result of resource polymorphism (Skulason and Smith 1995; Skulason et al. 1999; Snorrason and Skulason 2004). It is clear that morphologically similar morphs have evolved repeatedly and independently in different lakes (Gislason et al. 1999). For example, small benthic Arctic charr are found in a number of locations throughout Iceland (Sigursteinsdottir and Kristjansson 2005), most likely in response to specific lava habitats (Fig. 3). This evidence discounts the most likely alternative hypothesis, which proposes repeated invasions of genetically different arctic charr populations into the lakes.

Fig. 3 A small benthic artic charr, *Salvelinus alpinus*, from Thingvallavatn, Iceland to show details of dark body coloration, rounded head shape and subterminal position of the mouth (photograph by David Noakes)

Differentiation within the species is sympatric (intralacustrine), and occurs repeatedly, independently and (probably) convergently in different lakes. Phenotypic plasticity certainly seems to be a part of this process (Riddell and Leggett 1981; Wimberger 1994; DeWitt et al. 1998; Price et al. 2003; Sih et al. 2004a, b), but the extent of that is yet to be determined.

We have proposed a model (DeKerckove et al. 2006) with a mechanism for sympatric differentiation, based on initial behavioral differences. Those behavioral differences reinforce morphological (and other) differences, leading eventually to reproductive isolation between morphs with alternative foraging and social tactics. A critical feature of the model is the pattern of fitness benefits (=growth) for juveniles. We have established by a series of laboratory and field studies that young brook charr behave in one of two ways, “movers” or “stayers”, based upon foraging and social behavior. Movers forage while swimming about and show low levels of agonistic behavior. Stayers are central place foragers and show high levels of agonistic behavior. The fitness distribution of these young brook charr is bimodal, in that fitness of movers and stayers appears to be about equal. The bimodal pattern we observed in young brook charr is produced by the model only if it incorporates the full set of variables, suggesting that this is a consequence of multiple, subtle mechanisms. We see the initial stages of this process in the alternative foraging and social tactics of juvenile brook char, with consequent benefits to the growth of the young behaving either as movers or stayers. Those differences do not progress beyond those initial stages in brook charr in streams (Imre et al. 2001, 2002), because the environmental conditions encountered by brook charr in streams are too variable and unpredictable from year to year (Curry et al. 1994, 1995, 1997, Noakes and Curry 1995; McLaughlin and Grant 2001). This means that the initial behavioral differences cannot be reinforced by reproductive isolation between those tactics selected to reproduce in unique spawning locations. Streams are inherently unstable in both space and time, with fluctuations in spawning site characteristics and locations as a result of changes in water flow, erosion, sediment transport and bedload changes (Curry et al. 1994; Clément 2003). Fish within a stream can encounter a wide range of water current velocities, temperature and prey availability over very small spatial and temporal scales.

The conditions found in lakes, in contrast, provide relatively greater long-term stability of the physical habitat. Charrs, like many salmonid fishes, are characterized by philopatry in their spawning behavior (Noakes and Curry 1995). Spawning habitats in lakes are often site-specific, with significant consequences for early development, including behavior (Gunn and Noakes 1986, 1987; Curry et al. 1995). For example, the presence and specific qualities of groundwater at spawning sites can produce particular physico-chemical conditions for the developing embryos. Those conditions will have significant effects on early development and emergence time of the young at each site. The spawning segregation of polymorphic charr to site-specific sites would lead to enhanced differentiation among the morphs within the lake, and eventually the increasing degrees of reproductive isolation seen in different Icelandic lakes (Skulason et al. 1989b; Gislason et al. 1999).

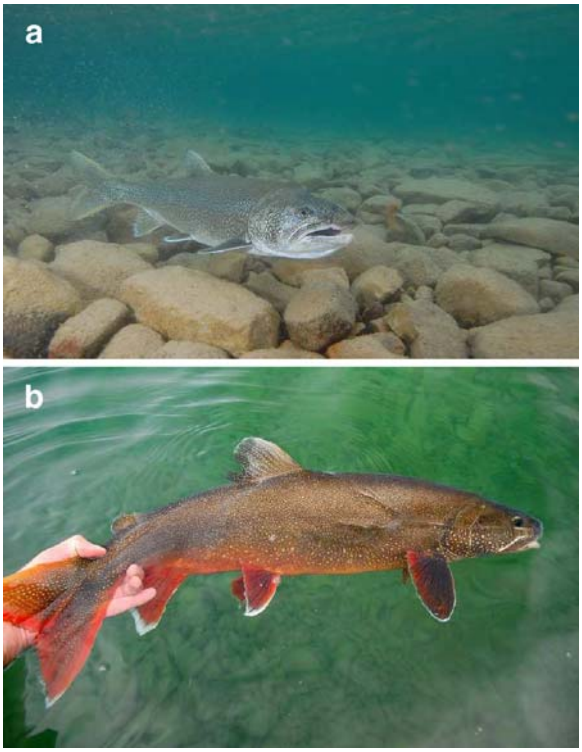

Fig. 4 **a** Piscivorous morph of lake charr, *Salvelinus namaycush*, from Great Bear Lake, Northwest Territories, Canada. Note the large terminal mouth, uniform gray coloration and relatively narrow caudal peduncle. (photo by Craig Blackie). **b** Benthivorous morph of lake charr, *S. namaycush*, from Great Bear Lake, Northwest Territories, Canada. Note the relatively small, somewhat subterminal mouth and red coloration on the fins and body. (photo by Craig Blackie)

This would certainly lead us to predict that we should find sympatric trophic polymorphism in charr species living in lakes, but not in streams. Tests of this prediction are still very much in progress, but the results thus far are entirely in agreement with the prediction. Lake charr in Great Bear Lake, a large, relatively undisturbed lake in arctic Canada show clear evidence of sympatric trophic morphs (Fig. 4) (Blackie et al. 2003; Alfonso 2004). There is also evidence, although it is less clear as a consequence of human disturbances, of similar polymorphism of lake charr in Lake Superior in the Laurentian Great Lakes. The multitude of populations of various charr species in lakes and rivers provides a wealth of opportunities to further test the predictions of our model in these and other species.

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