

Developmental rate: A unifying mechanism for sympatric divergence in postglacial fishes?

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Abstract Morphologically divergent ecotypes arise in fish populations on postglacial time scales, and resource polymorphisms are often invoked to explain their origin. However, genetic recombination can constrain the ability of divergent selection to produce reproductive isolation in sympatry. Recombination breaks up favorable combinations of traits ("adaptive suites") if individual traits are affected by different loci. Recombination also breaks up any association between traits under divergent selection and traits contributing to reproductive isolation. Thus, ecological speciation in the absence of preexisting barriers to gene flow is more likely when pleiotropy minimizes the number of loci involved. Here, we revisit research conducted by Carl Hubbs in the early 1900s on the effects of developmental rate on morphological traits in fishes. Hubbs' work provides a mechanism to explain how sympatric divergence by trophic polymorphism can occur despite the challenges of recombination. We consider the implications of Hubbs' observations for ecological speciation with gene flow in fishes, as well as rapid evolution in captive fish populations [*Current Zoology* 58 (1): 21–34, 2012].

Keywords Pleiotropy, Resource polymorphism, Selection-recombination antagonism

1 Introduction

Freshwater fishes in high-latitude postglacial lakes have proven to be fruitful systems for studying the origins of ecotypic diversity and divergence (Behnke, 1972; Schluter, 1996; Taylor, 1999). Postglacial lacustrine environments offer conditions that appear to promote divergence and coexistence of intraspecific ecotypes, including open niches due to the depauperate fauna and predictably discrete (littoral versus limnetic) habitats (Schluter and McPhail, 1993; Robinson and Wilson, 1994). As a result, a wide range of fish taxa show sympatric coexistence of discrete ecotypes, including representatives from the families Centrarchidae, Cyprinidae, Gasterosteidae, Osmeridae, and Salmonidae (including Coregoninae and Salmoninae), among others (reviewed in Robinson and Wilson, 1994; Schluter, 1996; Taylor, 1999).

The most commonly observed form of ecotypic divergence found in postglacial fishes is between benthic (littoral) and pelagic (limnetic) niches (Robinson and Wilson 1994). Robinson and Parsons (2002) reviewed 36 cases of sympatric pelagic and benthic ecotypes in

six families of freshwater fishes and found predictable morphological divergence between the forms functionally related to swimming performance and feeding morphology. When compared to benthic ecotypes, pelagic ecotypes tend to have smaller fins placed higher on the body, a longer caudal peduncle that is narrower in height but wider in cross section, a more slender body form with a smaller head, a less robust, terminal or up-turned mouth, and finer, more abundant gill rakers. These traits have been interpreted to be beneficial for the pelagic lifestyle of open-water cruising and feeding on small plankton, as opposed to the benthic life style of burst swimming and feeding on larger, harder benthic prey (Robinson and Parsons, 2002). Additionally, sympatric ecotypes often differ in eye size relative to body size, which is also likely related to their trophic ecology (Knudsen et al., 2006, Barrette et al., 2009), although the direction of divergence is less predictable (Willacker et al., 2010).

One of the most striking examples of ecotypic divergence in postglacial fishes is the coexistence of four distinct morphs of Arctic char *Salvelinus alpinus* in Thingvallavatn, Iceland. Two benthic ecotypes (dwarf

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and large), a piscivorous ecotype, and a planktivorous ecotype are all found within this 84-km² lake (Sandlund et al., 1992; Snorrason et al., 1994). The ecotypes are distinguished by a number of traits, including morphology, coloration, body size, and life history (Skúlason et al., 1989a, b; Sandlund et al., 1992). Another well-known example is the three-spined stickleback *Gasterosteus aculeatus*, which has repeatedly split into benthic and limnetic ecotypes in lakes of western British Columbia, Canada. Benthic ecotypes differ from limnetic ecotypes by attaining larger body size and having fewer and shorter gill rakers, a deeper, more robust body shape, and a wider mouth (McPhail, 1993); this species also shows parallel rapid evolution in body armor (e.g., Barrett et al., 2009), a pattern unique among postglacial fishes. A third well-documented example is lake whitefish *Coregonus clupeaformis*, which has independently split into ‘dwarf’ (limnetic) and ‘normal’ (benthic) forms in postglacial lakes in Maine (USA) and Québec (Canada). The primary morphological differences between the forms are gill raker counts and size at maturity (Bernatchez and Dodson, 1990), but other differences include pectoral fin length, caudal peduncle length, and maxillary length (Lu and Bernatchez, 1999).

Other forms of resource polymorphism, although less common, have also been documented in postglacial fishes. Blackie et al. (2003) and Alfonso (2004) identified morphological divergence between piscivorous and insectivorous ecotypes of lake char *S. namaycush* in Great Bear Lake, with the piscivorous form possessing longer snout and jaws, more slender caudal peduncle and mid-body depth, and smaller pectoral fins. Morphological differences between profundal and shallow-water forms in postglacial fishes have also been recognized. Profundal and shallow lake char from Great Bear and Great Slave lakes differ in head size, jaw length, body depth, caudal peduncle depth, eye position, and lipid content (Zimmerman et al., 2006, 2007). In the European whitefish *Coregonus lavaretus*, profundal morphs possess fewer and shorter gill rakers, deeper bodies, longer pectoral fins, and larger eyes (Kahilainen and Østbye, 2006; Kahilainen et al., 2011). Profundal morphs of Arctic char in Fjellfrøsvatn, Norway, have larger eyes, heads, and fins, and more slender caudal peduncles than their shallow counterparts (Klemetsen et al., 2002).

The young age of postglacial lakes (e.g., Thingvalavatn, ca. 9,500 years; Saemundsson, 1992) has prompted much study of how divergent intraspecific ecotypes came to coexist over such a short evolutionary

time scale. It is possible that the morphs are not genetically distinct, instead arising from a single random mating population with environmental variation the only source of phenotypic diversity (Taylor, 1999). However, a number of studies have demonstrated a heritable component to the traits of interest (e.g., Hindar and Jonsson 1993; Klemetsen et al., 2002), and in some cases, researchers have identified quantitative trait loci associated with ecotypic divergence (e.g., Peichel et al., 2001, Rogers and Bernatchez, 2005). When there is a heritable basis to phenotypic divergence, two alternative hypotheses could explain the coexistence of different morphs: divergence in allopatry followed by immigration, or divergence with gene flow (Smith and Todd, 1984). Genetic data are necessary to distinguish these hypotheses in the absence of a good fossil record.

In some cases the allopatric model of divergence is supported, such that different forms are genetically divergent from each other and have closer relatives in different lakes (e.g., Bernatchez and Dodson, 1990; Bernatchez et al., 1999) while in other cases genetic evidence suggests sympatric divergence, with different forms within a lake being more closely related to each other than to their respective forms in other lakes (e.g., Taylor and Bentzen, 1993; Bernatchez et al., 1999; Gíslason et al., 1999; Østbye et al., 2006; Palkovacs et al., 2008). Some species demonstrate a mosaic of allopatric and sympatric origins of ecotypes across their range (Bernatchez et al., 1999), with both vicariant history and more recent ecological and demographic processes contributing to morphological and genetic divergence (Barrette et al., 2009; Kapralova et al., 2011). In the context of ecological speciation, the situation where ecotypes originate in sympatry is of the greatest interest and will remain the focus of this paper. There is considerable controversy regarding use of the term ‘sympatric’ when discussing divergence and speciation (Fitzpatrick et al., 2008; Mallet et al., 2009). We use the term to refer to situations where gene flow is not restricted by physical barriers (e.g., intralacustrine).

2 Evolution of Reproductive Isolation by Resource Polymorphism

Resource polymorphism is the most commonly offered explanation for the coexistence of sympatrically diverged ecotypes in postglacial lakes (Smith and Todd, 1984; Jonsson and Jonsson, 2001; Noakes, 2008). This hypothesis states that postglacial aquatic systems, depauperate in fish species, provide ‘open niches’ that promote polymorphism in phenotypes related to trophic

ecology. Intraspecific competition drives divergent selection, ultimately resulting in either a stable polymorphism or speciation, depending on how much gene flow between forms occurs (Skúlason and Smith, 1995; Smith and Skúlason, 1996). Central to ecological divergence via resource polymorphism is reinforcement, where intermediate phenotypes have lower fitness (Schluter, 2000). Support for reinforcement is suggested in laboratory experiments with stickleback *Gasterosteus aculeatus* (Hatfield and Schluter, 1999), in findings of higher embryonic mortality in hybrids between ecotypes in lake whitefish *Coregonus* spp. (Bernatchez et al., 1999, 2010) and Arctic char (Hindar and Jonsson, 1993), and in reduced growth rates of juvenile brook char *S. fontinalis* showing intermediate foraging behavioral tactics (McLaughlin et al., 1999).

There are theoretical challenges to the efficacy of resource polymorphism as a mechanism for ecotypic divergence, however. These challenges stem from genetic constraints, and in particular, the antagonistic effects of recombination (Dobzhansky, 1951; Mayr, 1963; Felsenstein, 1981). Benthic and pelagic ecotypes tend to differ at a complex suite of traits, resulting in integrated phenotypes that enhance fitness in their respective environments (Robinson and Parsons, 2002). Such quantitative trait variation likely arises from a mixture of environmental and genetic factors, with heritable variation thought to be due to a number of genes dispersed throughout the genome (e.g., Derome et al., 2006, St-Cyr et al., 2008). In early stages of divergence, recombination would have prevented the evolution of such co-adapted gene complexes, and selection would need to be unrealistically strong to result in divergence in the absence of a pre-existing mechanism of reproductive isolation (Bolnick and Fitzpatrick, 2007).

The evolution of reproductive isolation in resource polymorphism scenarios is even more challenging. Some form of assortative mating is required to initiate divergence. In Felsenstein's (1981) 'two-allele' model for sympatric speciation, different alleles determine mating preference for a given ecotype (e.g., A_1A_1 individuals would prefer to mate with a 'pelagic' type individual, and A_2A_2 individuals would prefer to mate with a 'benthic' type individual). However, unless the locus for mating preference is tightly linked to the locus or loci for ecotype, recombination would break down the association between mating preference and ecotype, preventing divergence unless selection against intermediate types is extremely strong (Felsenstein, 1981). In the 'one-allele' model, substitution of the same allele in

both diverging daughter populations causes individuals to prefer to mate with individuals phenotypically similar to themselves. This model readily permits sympatric speciation because each daughter population fixes the same allele, so that recombination between the mating preference locus and ecotype does not disrupt divergence; however its biological realism is often doubted (Gavrilets, 2004; Bolnick and Fitzpatrick, 2007). In addition, neither of these models precludes the effect of recombination in breaking down multi-trait, integrated phenotypes (i.e., in either scenario, gene flow would shuffle traits, such that production of pure 'pelagic' and 'benthic' types would occur infrequently), calling into question how easily individuals could choose mates based on ecotype.

More recently, Via and West (2008; see also Smadja et al., 2008; Via, 2009) proposed a mechanism that would circumvent the challenges of recombination. They note that once reproductive isolation is initiated, recombination between daughter populations would be greatly reduced, resulting in much larger genomic regions that would be protected from selection-recombination antagonism ("divergence hitchhiking"). This process would reduce the degree to which pleiotropy or tight linkage is necessary for divergent selection to act efficiently. However, Feder and Nosil (2009) found that this mechanism would only result in substantial hitchhiking under limited conditions (low migration relative to the strength of selection and low effective population size, although these conditions become less limiting when multiple, but not numerous, loci are involved). Furthermore, some mechanism is still required to initiate divergence and to connect non-random mating to traits under divergent selection. Divergence hitchhiking is also more effective when selection can act sequentially on multiple traits as divergence proceeds (Via, 2009), rather than on integrated phenotypes at the initiation of divergence.

Numerous theoretical and numerical simulation approaches have demonstrated that the easiest way for reproductive isolation to evolve in sympatry is under mating/ecology pleiotropy or "magic trait" scenarios, where the locus controlling reproductive isolation (assortative mating) is the same trait controlling ecological divergence (Gavrilets, 2004, 2005). Such scenarios are often dismissed for being biologically unrealistic (Felsenstein, 1981; Coyne and Orr, 2004, Bolnick and Fitzpatrick, 2007), but some studies suggest that they might not be improbable in nature (Matsuo et al., 2007; Nosil and Schluter, 2011; Servedio et al., 2011), and diver-

gence hitchhiking increases the plausibility of such a mechanism resulting in substantial reproductive isolation (Via, 2009). Below we discuss how developmental rate (the absolute time to move from one defined developmental stage to the next), through its pleiotropic effects on fish morphology and association with temporal reproductive isolation, could mediate a “magic trait” scenario in the sympatric divergence of ecotypes in postglacial fishes.

3 Developmental Rate: A “Magic Trait”?

3.1 Effects of developmental rate on morphology

Prior to the development of molecular systematics, ichthyologists relied largely on morphometrics and meristics for phylogenetic reconstruction, and these remain important ichthyological tools to this day. Consequently, the degree to which morphologic and meristic differences represent genetic differences is of great importance to phylogenetic inference. Carl L. Hubbs, a prominent ichthyologist of the early to mid-1900s, conducted numerous studies of environmental effects on morphometric and meristic traits commonly used in systematic ichthyology (reviewed in Hubbs, 1926; Barlow, 1961). He discovered that a large number of morphological traits in fishes varied directly with developmental rate, including meristic counts (numbers of scales, gill rakers, fin rays, vertebrae), relative proportions (head size, eye size, fin size), and number/size of plates and spines. These effects were expressed regardless of the factor that influenced developmental rate (e.g., temperature, salinity, dissolved oxygen concentration, egg size). The relationship between latitude and vertebral count, thought to be attributable to temperature variation, has long been recognized by ichthyologists (‘Jordan’s rule’; reviewed in McDowall, 2008; see also Yamahira and Nishida, 2009). However, based on experimental results within populations and observations of populations across geographical clines, Hubbs documented a more general pattern: fishes subject to slower development have proportionately smaller eyes, heads, maxillaries, and fins, and greater meristic counts (Table 1), although exceptions were also noted (Hubbs, 1926; Barlow, 1961).

A model to explain these observations, initially proposed by Hubbs (1926) and further developed by Barlow (1961) and Lindsey and Arnason (1981), frames morphological outcomes in terms of relative rates of two different processes: growth and differentiation. The result depends on how far one of these processes has

gone when it is terminated by the attainment of a critical threshold by the second process. For example, vertebrae number could be greater in more slowly developing individuals because the differentiation phase takes longer, thus allowing more time for greater growth and providing a larger template (perhaps via greater number of cells) for somitogenesis (Fig. 1A, after Lindsey and Arnason 1981). Species or population differences in sensitivity of these processes to factors controlling development can account for exceptions from the general pattern described above, including nonlinear effects (Barlow 1961, Lindsey and Arnason 1981). Although this model provides little in the way of actual developmental mechanisms, it can successfully explain the results of a wide range of experiments on temperature effects on meristic counts (Lindsey and Arnason 1981, Swain and Lindsey 1986). Allometric growth, when coupled with differences in developmental rate, could readily result in differences in proportion as long as different body components do not respond isometrically to variation in developmental rate (Fig. 1B, see also Gould 1966, 1977). Modern empirical work continues to demonstrate the importance of developmental heterochrony in mediating environmentally induced morphological variation (Johnston, 2006; Martell et al., 2006).

Lindsey and Arnason’s (1981) model has been considered in the context of stock structure and genetic relationships among ecotypes (Foote et al., 1999; Swain and Foote, 1999), but the implications of Hubbs’ work on developmental rate for the origin of sympatric ecotypic divergence have largely been overlooked. In the following section we describe a verbal model in which developmental rate provides a unifying mechanism for the evolution of ecotypic divergence of postglacial fishes in sympatry. The pleiotropic effects of developmental rate overcome the challenges recombination poses to sympatric divergence, both in terms of the evolution of multi-trait, integrated phenotypes (“adaptive suites,” Singer and McBride, 2010) and in the evolution of reproductive isolation among individuals possessing different adaptive suites.

3.2 Model for ecotypic divergence via developmental rate heterogeneity

By definition, the ancestral population must be more or less monomorphic, or exhibiting low levels of morphological variation that is distributed continuously. In the model, an ancestral population colonizes a new postglacial lake where it experiences novel environmental conditions. For simplicity, we will use

Table 1 Traits involved in resource polymorphism (modified from Robinson and Parsons 1996) and general effects of slower developmental rate as summarized in Hubbs (1926) and Barlow (1961), unless otherwise noted. B = benthic, P = pelagic

Trait	Direction of divergence	Hypothesized function	Effect of reduced developmental rate
Paired fin size	B: larger P: smaller	B: maneuverability P: reduced drag	Smaller
Paired fin location	B: lower P: higher	B: burst swimming P: reduced drag	Effect observed, general direction unclear ¹
Body shape	B: robust P: streamlined	B: burst swimming P: reduced drag	Less robust ²
Head size	B: larger P: smaller	B: burst swimming P: reduced drag	Smaller
Caudal peduncle depth/width	B: deeper/narrower P: shallower/wider	B: burst swimming P: open-water cruising	Effect observed, general direction unclear ¹
Peduncle length	B: shorter P: longer	B: burst swimming P: open-water cruising	Longer
Mouth orientation	B: subterminal P: terminal or up-turned	B: benthic prey P: pelagic prey	Effect observed, general direction unclear ³
Mouth bones and muscles	B: robust P: reduced	B: large, hard prey P: small, soft prey	Unclear ⁴
Gill raker number/density	B: lower P: higher	B: reduced clogging P: planktivory	Higher
Gill raker length	B: shorter P: longer	B: reduced clogging P: planktivory	Longer? ⁵
Eye diameter ⁶	B: equivocal P: equivocal	B: large eyes – seeing prey in structurally complex habitat P: large eyes – seeing smaller prey	Smaller

¹ Temperature effects observed in juvenile chum salmon, Beacham (1990); genetic x rearing environment effects detected in profundal and littoral Arctic charr, Klemetsen et al. (2002).

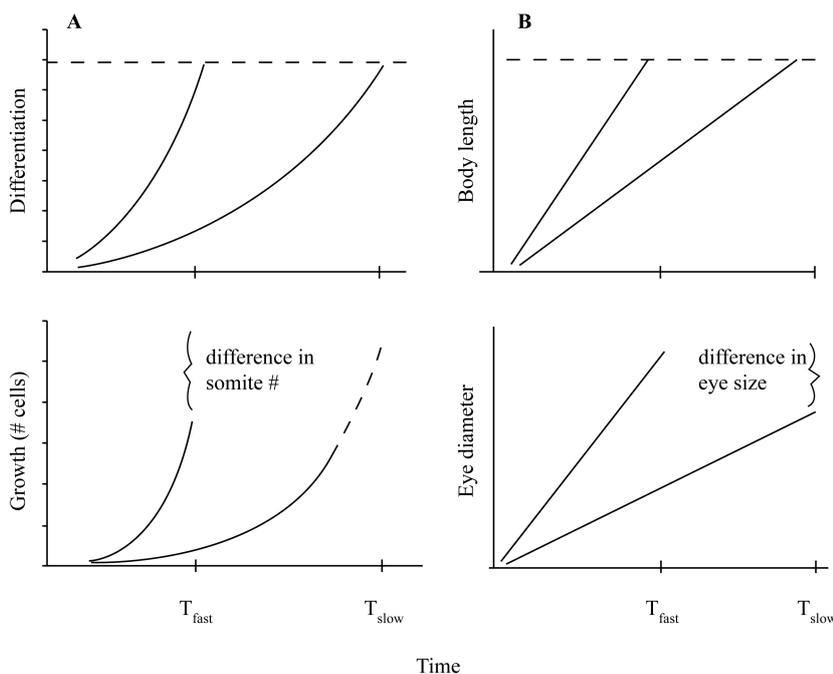
² Beacham (1990).

³ Rearing under common temperature resulted in sub-terminal mouths for both dwarf and normal Arctic char although genetic differences remained; Hindar and Jonsson (1993).

⁴ Pumpkinseed sunfish from a slower growing population had greater jaw ossification at earlier developmental stages; Arendt and Wilson (2000).

⁵ Captive-reared sockeye salmon (with faster development) had fewer and shorter gill rakers than wild parents; McCart and Andersen (1967).

⁶ Eye size was not considered by Robinson and Parsons (2002); see Willacker et al. (2010).

**Fig. 1** Effect of developmental rate on meristic and morphometric characters

A. Meristic character: the amount of differentiation achieved sets the end point (dashed line, top panel) for the developmental phase. Fast developers (left-hand line) reach this endpoint more quickly than slow developers (right-hand line), resulting in less growth (e.g., fewer number of cells) available for somitogenesis (bottom panel), and thus lower meristic counts. After Lindsey and Arnason (1981). **B.** Morphometric character (e.g., eye size): a given body length (top panel) is attained more quickly for fast developers (left-hand line) than slow developers (right-hand line). At the same time, eye diameter increases more quickly for fast developers (bottom panel), resulting in a larger eye size for a given length in fast developers.

temperature as the important variable, but other conditions affecting developmental rate, such as dissolved oxygen or salinity (less relevant in this freshwater example), could play a similar role. Heterogeneity in thermal regimes experienced by developing offspring in the novel environment leads to heterogeneity in developmental rates, resulting in increased morphological variation. Importantly, developmental rate affects suites of morphological traits such that environmental variation consistently results in integrated ‘fast’, ‘intermediate’ and ‘slow’ morphologies. Fast-developing fishes would resemble the benthic ecotype, showing larger fins, a more robust body, larger head size, lower number and density of gill rakers, and smaller eyes (Table 1). More slowly developing fishes would resemble the pelagic ecotype, and individuals experiencing intermediate developmental rates would show intermediate phenotypes.

According to the theory of resource polymorphism, intraspecific competition, enhanced by lack of interspecific competition in depauperate postglacial lakes, would favor individuals occupying the tail ends of the distribution of morphologies, with intermediate individuals showing decreased fitness relative to fast and slow morphologies. Without any mechanism for the inheritance of morphological differences, no divergence would take place. However, the pleiotropic effects of developmental rate on morphology could also serve to link reproductive isolation to morphological divergence, via the effect of spawning time on the thermal regime experienced by incubating eggs and embryos. The heritability of spawning time in fishes has been demonstrated in a number of populations (e.g., Su et al., 1997; Smoker et al., 1998), ranging from 0 to 1 with a median of approximately 0.5 across salmonids, for example

(Carlson and Seamons, 2008). Similarly, studies have documented sufficient genetic variation in introduced populations to allow rapid evolution in spawning time (e.g., Quinn et al., 2000). Given sufficient variation in thermal regime across the range of spawning time, this could create a situation where disruptive selection on morphology leads to reproductive isolation via selection against individuals with intermediate spawning time (Fig. 2).

We note that the trait actually under divergent selection (thus the true ‘magic trait’; Servedio et al., 2011) is spawning time, but the ‘ecology’ component of the mating/ecology pleiotropy is due to the subsequent effects of spawning time on morphological phenotype, as mediated by developmental rate. Once reproductive isolation is initiated, divergent selection could then act directly on developmental rate (often heritable in fishes; Easton et al., 2011 and references therein) and on the reaction norms of individual morphological traits on developmental rate variation to further refine and canalize divergent morphologies. Spawning site heterogeneity, if coupled with differences in thermal regime due to variation in groundwater inputs, could produce a similar mode of ecotypic divergence. Although the heritability of spawning site is less apparent than that of spawning time, this is a plausible mechanism given the high incidence of philopatry in fishes, particularly salmonids. However, this becomes micro-allopatry, so might be considered by some irrelevant to a discussion of sympatric divergence.

That developmental rate has such far-reaching consequences for morphology has profound, yet not fully appreciated, implications for sympatric divergence by resource polymorphism. Nearly all of the traits identified

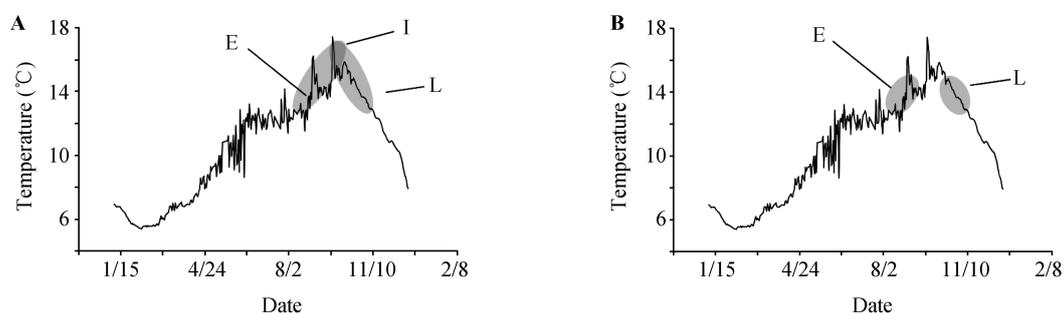


Fig. 2 Reproductive isolation by allochrony via pleiotropic effects of developmental rate on morphology

A. Newly colonized ancestral population, with spawning period (shaded grey area) shown against a hypothetical lacustrine thermal regime. Different spawning time leads to different thermal regimes for incubation. Offspring of early spawners (E) develop more quickly, leading to a fast (~benthic) morphology, while offspring of late spawners (L) develop more slowly, leading to a slow (~pelagic) morphology (see text and Table 1). Offspring of intermediate spawners (I) develop intermediate morphology. **B.** When spawning time is heritable, generations of selection against intermediate morphologies leads to reproductive isolation by allochrony.

as being involved in resource polymorphism in post-glacial fishes (e.g., benthic/limnetic forms, Robinson and Parsons, 2002; piscivorous/insectivorous forms, Blackie et al., 2003; profundal/shallow forms; Klemetsen et al., 2002; Kahilainen and Østbye, 2006; Zimmerman et al., 2006, 2007) are influenced by developmental rate in some species or populations (Table 1). This suggests that these adaptive suites could be under the control of only a few loci associated with developmental rate, greatly increasing the likelihood that these ecotypes could have diverged in sympatry over post-glacial timescales.

3.3 Model predictions and empirical support

Clearly, it is difficult to test a model for a process that occurs over decadal to millennial time scales; however some of the model's assumptions and predictions can be assessed. The model assumes that a colonizing population experiences a novel and more heterogeneous thermal regime during spawning than that experienced in its ancestral habitat. In many fishes, spawning is cued to a large degree by photoperiod (e.g., Beacham and Murray, 1988), and temperature should vary over finer spatial scales than does photoperiod, particularly during times of climate dynamism such as that accompanying the end of the last glacial period. Climatic niche shifts (including temperature) have been documented in a number of anthropogenic range extensions in fishes (Lauzeral et al., 2011), although it is less clear how often they have accompanied natural colonization events. Regional variation in underlying geology affects the nature of groundwater inputs, which have significant effects on thermal regimes (e.g., Poole and Berman 2001) and in some cases, on the occurrence of ecotypes (e.g., the small benthic form of Arctic char in Iceland; Sigursteindóttir and Kristjánsson, 2005). In either case, our model does not specify that the novel thermal regime be outside the range experienced in the ancestral habitat; it just requires that the regime be sufficiently novel that early and late spawners experience different enough developmental rates to induce novel phenotypic variation.

The developmental-rate model predicts that reproductive isolation occurs initially via allochrony. We are not aware of any comprehensive evaluation of the role that temporal isolation has played in reproductive isolation among ecotypes across species of postglacial fishes. Reproductive isolation among ecotypes often consists of differences in both spawning habitat and time (e.g., chars, reviewed in Jonsson and Jonsson, 2001). In other cases spawning time is the only apparent source of re-

productive isolation (e.g., ciscoes *Coregonus* spp., Ohlberger et al., 2003; Schulz et al., 2006; kokanee and sockeye salmon *Oncorhynchus nerka*, although with considerable temporal overlap, Wood and Foote, 1996). Evaluating this prediction is tricky, because allochrony can arise via divergent selection on other traits, such as habitat selection (Yamamoto and Sota, 2009). Furthermore, other pre- or post-zygotic isolating mechanisms might have arisen after reproductive isolation via allochrony, maintaining reproductive isolation following subsequent relaxation of temporal separation. However, it is compelling that one of the pioneering studies of ecotypic divergence in salmonids focused on differences in spawning time and resulting environmentally-induced variation in gill raker morphology (Frost, 1965; reviewed in Klemetsen, 2010).

The model also predicts that few loci should be involved in ecotypic divergence, at least initially (see also Danzmann et al., 1991). Leary and colleagues identified an allele at a regulatory locus (*Pgm1-t*) in rainbow trout *O. mykiss* that caused individuals to develop more quickly and have reduced meristic counts, greater size-at-age, and earlier maturity (Allendorf et al., 1983, Leary et al., 1984). This cis-acting regulatory locus controls the expression of a locus (*Pgm-1*) coding for the enzyme phosphoglucomutase locus in liver. Embryos with liver *Pgm-1* expression hatch earlier than embryos without liver *Pgm-1* expression. These differences apparently result from increased flux through glycolysis in embryos with liver *Pgm-1* expression while they are dependent on the yolk for energy. The amount of morphological divergence between full-sibs with different genotypes at *Pgm1-t* was similar to that between subspecies of cutthroat trout *O. clarki* (Leary et al., 1984). This example suggests that divergent selection at a single locus could result in the rapid origin of distinct ecotypes.

More recent work has focused on gene expression profiling ("transcriptomics") in order to identify genes that might be involved in ecotypic divergence; such studies often find many (on the order of 100s) candidate loci (e.g., Derome et al., 2006; St-Cyr et al., 2008). However, these loci are often related to just a few functional groups (Bernatchez et al., 2010; Goetz et al., 2010), and when gene-mapping work is conducted, many differentially expressed genes are found to be co-located to several chromosomal "hotspots" involved in divergence (Bernatchez et al., 2010). Future transcriptomics studies might prove particularly useful in uncovering the role of physiological differences, which

can be difficult to measure in the field, in ecotypic divergence (Pavey et al., 2010). Quantitative genetics studies, particularly those that estimate genetic covariances (the G-matrix approach, Arnold et al., 2008) will also be crucial for understanding how adaptive suites diverge over postglacial timescales.

Finally, the model makes specific predictions about the incubation environments experienced by benthic versus pelagic ecotypes in the early stages of divergence: benthic individuals should develop more quickly than should pelagic individuals. Previous studies investigating the role of plasticity in ecotypic divergence among postglacial fishes have largely ignored temperature (or other factors affecting developmental rate such as egg size or dissolved oxygen concentration), instead focusing on habitat choice or feeding ecology (e.g., Robinson and Parsons, 1996; Parsons et al., 2010, but see LeBlanc, 2011). Therefore few studies provide the information needed to assess this prediction. Detailed natural history information from Thingvallavatn char do support the model outlined in Fig. 2, however. Benthic forms tend to spawn on the ascending limb of the lake thermograph (July–August), while pelagic forms spawn on the descending limb (September–November); the small benthic form shows a protracted spawning period extending from July into November (Skúlason et al., 1989a; Sandlund et al., 1992). Spawning site interacts with date to influence the temperature experienced by developing embryos, however. Unlike the pelagic forms, the benthic forms spawn in areas affected by upwelling ground water, which is colder than lake water in the summer but warmer than lake water in the fall, leading to a warmer incubation regime and earlier emergence (Skúlason et al., 1989a). Furthermore, small benthic morphs have the smallest eggs (Eiriksson et al., 1999; LeBlanc, 2011), which should lead to faster development (Valdimarsson et al., 2002).

These observations suggest that benthic forms, and in particular the small benthic form, of char in Thingvallavatn should develop more quickly than should the pelagic forms, as predicted by our model. However, it should be pointed out that in a resource polymorphism, selection against intermediate forms should lead to canalization of divergent phenotypes that were originally environmentally induced (Parsons et al., 2010), limiting our ability to assess historical processes from contemporary observations. When individuals were reared under the same thermal regime, somitogenesis was slower in dwarf benthic than large benthic form of Arctic char from Thingvallavatn (Sibthorpe et al., 2006), suggesting

that such canalization might have occurred (although maternal effects were not examined and rates of somitogenesis for planktivorous forms were not reported). Similarly, Johnston et al. (2004) did not detect rearing temperature effects on fast muscle fiber number in Thingvallavatn char, even though the dwarf benthic morph had fewer fibers than the large benthic and planktivorous morphs.

The mechanism for divergence in foraging behavior is a critical component missing from our model. Is there any evidence to suggest that developmental rate could link behavior and morphology along the benthic-limnetic axis of divergence? To the best of our knowledge, no studies have specifically addressed this question; however, energetic and behavioral polymorphisms of brook char have been well studied and may offer insight. Sacotte and Magnan (2006) found that lake-dwelling brook char that inherited a benthic swimming morphology also inherited increased capture and retention rates on benthic prey relative to their limnetic counterparts. In stream-dwelling brook char, two behavioral ecotypes have been identified (McLaughlin et al., 1999; Noakes, 2008): ‘movers,’ or individuals who display high rates of activity and aggression and feed high in the water column, and ‘stayers,’ who forage closer to the stream bottom and show decreased activity and aggression. Biro and Ridgway (2008) documented similar behavioral types (active versus sedentary) in lake-dwelling brook char. Differences in metabolic and intrinsic growth rates have been implicated in behavioral diversity, and in cases where individuals cannot meet their metabolic requirements where they are, habitat switching is a likely response (Morinville and Rasmussen, 2003; Biro and Ridgway, 2008). If individuals with pelagic-like morphologies are unable to feed efficiently in their natal (benthic) environment, they may be more likely to switch to a limnetic mode of living. Furthermore, to the extent that later metabolic rates might be correlated with early metabolic and developmental rates (see discussion in following section), the possibility that behavioral diversity arises as a pleiotropic effect of rate differences early in life deserves further study.

4 Conclusions and Further Implications

Numerous authors studying resource polymorphism in postglacial fishes have highlighted the importance of plasticity in generating the phenotypic variation upon which divergent selection can act (e.g., Robinson and Parsons, 1996; Skúlason et al., 1999; Adams and Huntingford, 2004; Klemetsen, 2010; Parsons et al., 2010).

Researchers, particularly those working on charrs, have further recognized the importance of heterochrony in the origin of ecotypes (e.g., the paedomorphic small or dwarf benthic form of Arctic char in Thingvallavatn, Skúlason et al., 1989b; Hindar and Jonsson, 1993; Eiríksson et al., 1999; benthivorous vs. planktivorous Arctic char in Loch Rannoch, Scotland, Adams and Huntingford, 2002). The salient feature of our developmental rate model is its ability to overcome selection-recombination antagonism, a potentially important but often over-looked challenge to sympatric divergence via resource polymorphism in postglacial fishes. The pleiotropic effects of developmental rate on morphology allow for divergent selection to act efficiently on adaptive suites, and the link between spawning time and thermal regime leads to pleiotropy between reproductive isolation and the suite of traits subject to divergent selection.

The multifaceted effects of developmental rate also have implications for contemporary evolution, particularly in the context of human-caused selection. Salmonid biologists have long been aware of the potential of domestication selection to lead to a “hatchery-type” phenotype in captivity (Helle, 1981; Hynes et al., 1981), and numerous studies have quantified similar suites of morphological differences between captive and wild populations of salmonids (e.g., Taylor, 1986; Fleming and Gross, 1989; Hard et al., 2000; Solem et al., 2006; Wessel et al., 2006; Yurtseva et al., 2010; Tiffan and Connor, 2011). Interestingly, most of the traits involved in wild-hatchery differences (body depth, caudal peduncle length and depth, head length, paired fin size, eye diameter) are those that are affected by developmental rate (Table 1). Swain et al. (1991) pointed out that much of the morphological difference between captive and wild fish could be due to phenotypic plasticity. Indeed, it is difficult to understand how hatchery populations could diverge from wild populations, independently and in repeatable ways over the short time frames (several generations) documented in these studies, without invoking plasticity (however, see Roberge et al., 2006 and Sauvage et al., 2010 for examples of rapid and heritable divergence in gene expression, mostly related to growth and metabolism, in captive-bred salmonids). Maternal effects could also play an important role; captive rearing often causes a decrease in egg size (LeBlanc, 2011) and an increase in egg size variation (Einum and Fleming, 2000a; LeBlanc, 2011) within a single generation, and egg size affects developmental rate (Valdimarsson et al., 2002) and morphology (LeBlanc, 2011). On one hand,

these observations imply that evolution by domestication selection may not be as pervasive or permanent as is often perceived. On the other hand, if these morphological traits are under the pleiotropic control of developmental rate, then unintended selection on developmental rate (or a covariate such as egg size) could efficiently cause rapid genetic divergence in morphology in captive populations.

In addition to developmental rate, juvenile growth and metabolic rates have important consequences for both morphological and life-history variation in fishes. Rapid growth (or higher metabolic rate; Trudel et al., 2001) can cause fish to mature early (Metcalf, 1998; Thorpe, 2007), possibly leading to paedomorphic retention of juvenile morphologies (e.g., proportionately larger eyes and fins), and rapidly growing fishes attain greater body depth and width per body length (Kause et al., 2003). It may be the case that differences in growth rate after exogenous feeding, mediated by juvenile rearing environment, are necessary to maintain morphological differences achieved during early development (Alexander and Adams, 2004). Differences in activity rate, including aggressiveness and other forms of foraging behavior, are thought to be important components of resource polymorphism (McLaughlin et al., 1999; Skúlason et al., 1999) and may lead to morphological divergence as well (Adams et al., 2003). Therefore, heterogeneity in later growth and metabolic rates might be more important than early developmental rates in the origin of some ecotypes (e.g., ‘dwarf’ versus ‘normal’ types; e.g., Eiríksson et al., 1999; Trudel et al., 2001; Helland et al., 2009).

How variation in early metabolic and developmental rate influences later metabolic and growth rates in fishes has not been well investigated; however, several studies point to the intriguing possibility that factors acting early in development can have lasting consequences for fish growth and life-history (see also Jonsson and Jonsson, 2009). In the wild, a correlation between developmental rate and growth rate could persist because of the ecological effects of more rapid development and early emergence, including acquisition of feeding territories and maintenance of social dominance (Einum and Fleming, 2000b; McCarthy et al., 2003). In addition, differences in egg size correlate with size and behavior at the onset of feeding, with larger eggs (which develop more slowly) producing larger, more active foragers (Benhaïm et al., 2003; LeBlanc et al., 2011). Other studies have found evidence for genetic and/or physiological bases for a connection between development and

later metabolic processes. Allendorf et al. (1983) found that individuals possessing the *Pgml-t* allele (resulting in faster development) also attained greater size-at-age and earlier sexual maturity. Rungrangsak-Torrissen et al. (1998) demonstrated that differential expression of trypsin isozymes in Atlantic salmon *Salmo salar* was induced by different temperatures at hatching and the onset of exogenous feeding and resulted in differences in conversion efficiency and growth rate that lasted throughout the juvenile period. In brown trout *S. trutta*, temperature at and immediately following yolk absorption influenced standard metabolic rate (Álvarez et al., 2006). Linkage mapping in steelhead/rainbow trout *O. mykiss* has shown that the major QTL for developmental rate (Easton et al., 2011) is also a major QTL for smoltification traits (Nichols et al., 2008), suggesting a genetic correlation between developmental rate and life history that also exists independent of ecological considerations.

We have proposed an important and multifaceted role for developmental rate variation in rapid ecotypic divergence in postglacial fishes, but this idea has not been explicitly tested. We hope that this review will stimulate further empirical work on the effects of developmental rate variation. For example, future work could address the following questions: 1) Can developmental rate variation in the lab induce divergent, integrated phenotypes that mimic those seen in pelagic/benthic ecotypes? 2) Can selection on developmental rate norms of reaction lead to divergence in multiple morphological traits? 3) Does early variation in developmental rate (e.g., induced by thermal variation) cause variation in metabolic rate later in life? 4) How much intralacustrine variation in incubation environment (temperature, dissolved oxygen) is experienced by colonizing fish populations? These and other questions regarding developmental rate should be considered in the context of both genetic architecture (including maternal effects, particularly those mediated by egg size, Leblanc, 2011) and ecological factors acting throughout a fish's lifespan, in order to gain a more integrative understanding of the mechanisms that generate and maintain ecotypic diversity in fishes.

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