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NEWS AND VIEWS

PERSPECTIVE

Adaptation genomics: next generation sequencing reveals a shared haplotype for rapid early development in geographically and genetically distant populations of rainbow trout

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Abstract

Local adaptation occurs when a population evolves a phenotype that confers a selective advantage in its local environment, but which may not be advantageous in other habitats. Restricted gene flow and strong selection pressures are prerequisites for local adaptation. Fishes in the family Salmonidae are predicted to provide numerous examples of local adaptation because of the high fidelity of returning to spawn in their natal streams, which results in highly structured populations, and the wide diversity of environments that salmonids have colonized. These conditions are ideally suited for producing a set of specialist phenotypes, whose fitness is maximized for one specific habitat, rather than a generalist phenotype similarly viable in several environments. Understanding patterns and processes leading to local adaptations has long been a goal of evolutionary biology, but it is only recently that identifying the molecular basis for local adaptation has become feasible because of advances in genomic technologies. The study of shared adaptive phenotypes in populations that are both geographically distant and genetically distinct should reveal some of the fundamental molecular mechanisms associated with local adaptation. In this issue of *Molecular Ecology*, Miller *et al.* (2012) make a significant contribution to the development of adaptation genomics. This study suggests that salmonids use standing genetic variation to select beneficial alleles for local adaptations rather than *de novo* mutations in the same gene or alternative physiological pathways. Identifying the genetic basis for local adaptation has major implications for the management, conservation and potential restoration of salmonid populations.

Keywords: ecological genomics, local adaptation, quantitative trait locus, rainbow trout, standing genetic variation

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Adaptation genomics

Adaptation and natural selection are at the very heart of evolutionary biology. Williams (1966) suggested that to explain adaptation, 'one should assume the simplest form of natural selection, namely that of alternative alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice'. The traditional view was that an adaptation would arise in a particular environment via a *de novo* mutation, and this novel allele would then be selected in that population. However, observations of parallel phenotypes in populations within a species and among closely related species demand a more complex explanation to account for the phenomenon of similar local adaptations. Many of the conceptual issues of local adaptation, such as the importance of natural selection, gene flow and other evolutionary forces, have been reviewed (Kawecki & Ebert 2004), and a strong case has been made for studying parallel local adaptations. Elmer & Meyer (2011) recognized that parallel phenotypes, or replicative adaptive radiations, may have three genetic bases: (i) the same mutation (allele) in a gene; (ii) a different mutation (allele) in the same gene; and (iii) mutations in different genes. There is evidence to support each of these schemes. For example, in threespine sticklebacks, the reduction in armour plating seen in different freshwater populations relative to their marine counterparts appears to be predominantly the result of repeated selection of pre-existing alleles in the *Ectodysplasin*-A gene (*Eda*), which occur at low levels in marine populations (Colosimo *et al.* 2005). In contrast, albinism in cavefish populations has been shown to be owing to independent loss of function mutations (i.e. different alleles) in the ocular and cutaneous albinism-2 gene (*Oca2*) (Protas *et al.* 2006). Moreover, the apparent parallel phenotypes of light and dark pigmentation in wild populations of *Peromyscus* sp. exhibit homologous and non-homologous genetic origins, resulting from independent mutations in the *McR1* and *Agouti* genes (Manceau *et al.* 2010). The development of genomic technologies, such as next generation sequencing, is enabling a better understanding of how organisms adapt to different environmental niches (Stapley *et al.* 2010). In particular, adaptation genomics allows us to ask how many genes are involved in an adaptation, what types of genetic variation are associated with an adaptation, and to what extent does adaptation rely on standing genetic variation as opposed to new mutations.

Local adaptation occurs when a population evolves a phenotype that confers a selective advantage in its local environment, but which may not be advantageous in other habitats (Williams 1966). Ideal conditions for local adaptation to occur include restricted gene flow between demes,

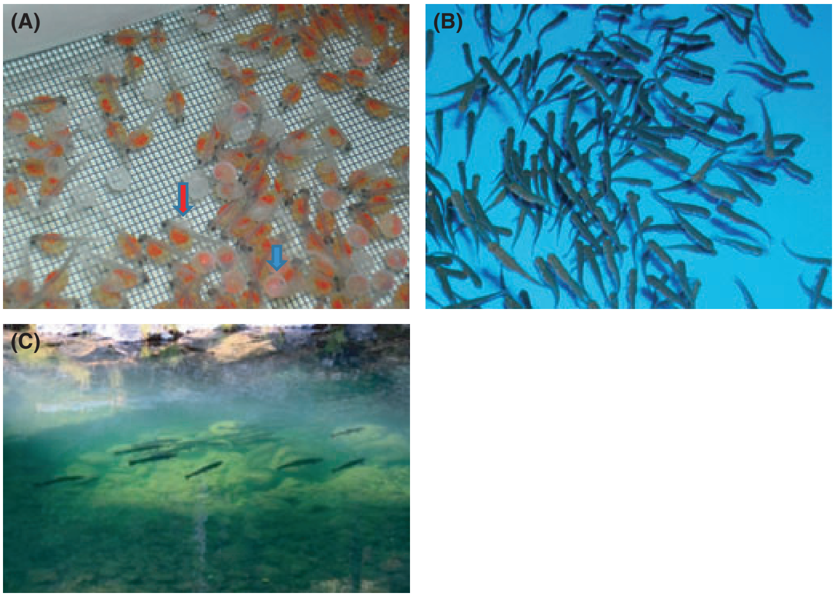

Fig. 1 Salmonid populations vary in rates of early development to optimize conditions for fry emergence. In some locations, early hatching rainbow trout (i.e. those with a fast development rate) are more likely to survive. This trait has been selected for in geographically and genetically distant populations of rainbow trout from standing genetic variation rather than by *de novo* mutations or alternative physiological pathways. (A) Shows hatched yolk sac fry (red arrow) and unhatched eggs (blue arrow). (B) and (C) Show fingerlings and wild rainbow trout, respectively.

genetic loci that contribute strong effects on fitness and strong selection pressures (Kawecki & Ebert 2004). The Salmonidae, (i.e. salmon, trout, charr, freshwater whitefish and grayling; Nelson 2006) are predicted to provide numerous examples of local adaptation because of their high fidelity of returning to spawn in their natal streams, which results in highly structured populations (Quinn 2005), and the wide diversity of environments the salmonids have colonized (Primmer 2011). These conditions are ideally suited for producing a set of specialist phenotypes, whose fitness is maximized for one specific habitat, rather than a generalist phenotype similarly viable in all environments (Taylor 1991; Fraser *et al.* 2011). It is quite common for sympatric 'ecomorphs' (e.g. dwarf and normal size lake whitefish (Bernatchez *et al.* 2010); resident and anadromous forms of Atlantic salmon (Birt *et al.* 1991); benthic and pelagic Arctic charr (Kapralova *et al.* 2011)) to coexist in the same watershed. But it has also been documented that salmonid populations, which are genetically distinct based on neutral markers, appear to share the same or similar local adaptations (Bernatchez *et al.* 1996; Taylor *et al.* 1996; Waples *et al.* 2004). Understanding the mechanisms by which these parallel local adaptations arise and dissecting their molecular basis are not only of central interest to evolutionary biologists, but also have practical implications for conservation biologists.

allel local adaptation for rapid early development

The period immediately after emergence from their gravel nests is a particularly challenging time for salmonids, and this is when the greatest mortality occurs (Elliott 1989). The time from fertilization to hatch, which is a measure of developmental rate, is associated with length of fry in pink salmon (Beacham *et al.* 1988) and larger size and earlier sexual maturity in some strains of rainbow trout (Allendorf *et al.* 1983). It has also been observed that there is selection against late emergence and small offspring in Atlantic salmon (Einum & Fleming 2000). It is not surprising then that variation in developmental rate has been observed in populations of rainbow trout (Robison *et al.* 1999) (Fig. 1). What is surprising is that two of the populations, Clearwater and Swanson, in which rapid rates of early development have been described, come from distant geographical locations and belong to distinct subspecies of *Oncorhynchus mykiss*. The Clearwater strain is from North Central Idaho and represents the inland subspecies, whereas the Swanson originated in Southcentral Alaska and is part of the coastal subspecies (Allendorf & Utter 1979). Clonal homozygous lines, produced by androgenesis or gynogenesis, are available for Clearwater and Swanson rainbow trout as well as other populations, and it has been shown that the variation in developmental rates in the clonal lines reflects what is observed in the wild populations from which they were derived (Robison *et al.* 1999). Quantitative trait loci (QTL) mapping identified a region of the genome that accounts for up to 30% of the observed developmental rate variation (Robison *et al.* 2001; Sundin *et al.* 2005; Nichols *et al.* 2007). Moreover, the QTL maps to the same location in the Clearwater and Swanson strains. However, it was not clear if the Clearwater and Swanson populations have evolved an increased rate of development from the same allele in the same gene, a different allele in the same gene or from different genes that by chance are located in the same part of the genome. Another possibility was that the OSU strain used in the QTL mapping studies actually imparted a slower developmental rate (Nichols *et al.* 2007). In this issue of *Molecular Ecology*, Miller *et al.* (2012) make a significant contribution to the development of salmonid adaptation genomics. They used a combination of laboratory crosses of homozygous lines of rainbow trout derived from natural populations, chromosome set manipulation, next generation sequencing and QTL mapping using RAD Tag SNPs (Miller *et al.* 2007; Baird *et al.* 2008) to identify a conserved haplotype that is associated with rapid early development in the Clearwater and Swanson strains of rainbow trout. This study suggests that these populations of rainbow trout used standing genetic variation in the species as a whole (Barrett & Schluter 2007) to select beneficial alleles for the local adaptation of rapid early development rate rather than *de novo* mutations in the same gene or alternative physiological pathways.

Looking forward

Identifying the genetic basis for local adaptation has major implications for the management, conservation and potential restoration of salmonid populations, many of which are threatened. For example, many attempts to transplant salmonids for restoration and enhancement purposes have failed (Waples 1991). Indeed, the use of hatcheries to supplement salmonid populations that have decreased because of overfishing, habitat destruction and the blockage of migratory routes may not be having the desired effect because of direct genetic effects caused by hybridization and introgression of hatchery stocks with local fish or more indirect effects, which result from changes in the gene pool of the stocked fish by selection for hatchery conditions. With the completion of a salmonid reference genome anticipated in 2012 (Davidson *et al.* 2010), studies such as the one reported by Miller *et al.* (2012) provide hope that genomics can make a positive contribution to the future of conservation genetics of salmonids (Allendorf *et al.* 2010).

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The author is interested in the evolution of salmonid genomes and how genomics can be applied to salmonid aquaculture and conservation.

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