

Summary and perspective on evolutionary ecology of fishes

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Abstract This special issue of Evolutionary Ecology provides ten papers that have been presented at a conference on Evolutionary Ecology of Fishes in 2009. In addition to briefly summarizing the main content of the papers which is related to adaptive radiations, processes of ecological divergence, and fisheries-induced evolution, we review and synthesize in short the recent advance in studies on evolutionary ecology of fishes. We conclude that fishes are excellent model systems to study evolutionary ecology of animals, and suggest three promising new research avenues; (1) the contribution of behavioural processes to evolution, in particular the consideration of animal personalities and predator–prey interactions, (2) metabolic physiology and parasite–host interactions as new niche dimensions to be considered for adaptive diversification, and (3) the opportunities for mechanistic understanding of adaptation and speciation emerging from new genetic tools.

Keywords Non-model systems · Ecological speciation · Behavioural interactions · Local adaptation

Introduction

On occasion of the 200th birthday of Charles Darwin (12 February 1809), and exactly 150 years after the first appearance of his most famous book “On the origin of species” (published on 24 November 1859), we invited researchers to an international conference

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titled “Evolutionary Ecology of Fishes: Diversification, Adaptation and Speciation” held in Erkner near Berlin (Germany) from 23 to 25 November 2009. Our call was well received and a total of 180 participants from 25 countries presented 81 talks and 65 posters. The unifying subject of all presentations was fish, but a broad variety of patterns and processes was discussed within the conceptual framework of evolutionary ecology. With ten papers, this special issue of Evolutionary Ecology inevitably presents only a small fraction of the work presented and discussed at the conference, but covers topics as diverse as adaptive radiation, ecological speciation, and fisheries-induced evolution. Here we begin with a summary of each contributed paper and then formulate a synthesis of the work in a larger context. We conclude that fishes are excellent model systems for studies on evolutionary ecology and propose three emerging research themes that provide innovative avenues for research.

Summary of presented papers

The first three papers in this issue elucidate patterns of adaptive radiations in fish related to monophyly, rapid diversification, strong phenotype-environment correlations and the utility of specific traits in alternative niches (Schluter 2000). Post-glacial adaptive radiations of the genus *Coregonus* in temperate regions have been studied extensively (Østbye et al. 2005; Mehner et al. 2010; Bernatchez et al. 2010; Winkler et al. 2011), but there is still a scarcity of information from East-European and western and central Asia species. Bochkarev et al. (2011) studied the evolutionary history and diversification between populations of south-Siberian whitefish *Coregonus pidschian* by comparing morphology, ecology and genetics (mtDNA). They suggest that water bodies in the southern part of Siberia represent a secondary contact zone characterized by hybridization between lineages of *C. pidschian*, a process recently suggested also for the Alpine whitefish lineages (Hudson et al. 2011). Kahilainen et al. (2011) hypothesized that adaptive radiations of *Coregonus* populations are reflected by gill-raker divergence. They argue that there is a feedback-loop between gill-rakers and selection, because competition for scarce resources intensifies natural selection, leading to stronger divergent selection for the adaptive traits. The common concept of littoral-pelagic divergence in post-glacial evolution of sympatric freshwater fishes (Schluter 1996) can be extended to the profundal (deepwater bottom) habitat, because profundal populations had fewer gill rakers than populations from littoral and pelagic habitats. Resource polymorphisms and phenotype-environment correlations were also described in a polymorphic Scandinavian population of *Salvelinus alpinus* (Knudsen et al. 2011). There was a close relationship between foraging behaviour, functional trophic morphology, and temporally integrative diet use as indicated by stable isotopes and the parasite composition. The authors conclude that resource-based divergent selection may be mediated by parasites, in particular in the benthic habitat where the diet is less diverse and hence morphological specialization almost impossible.

The next four papers of this special issue address single processes in ecological speciation that may shift divergence between populations along the continuum from seemingly panmictic conditions to complete reproductive isolation (Hendry 2009). Eizaguirre et al. (2011) show the action of homogenizing selection on immunogenetics (major histocompatibility complex, MHC) diversity within habitat type, and diverging selection between habitat types in three-spined sticklebacks (*Gasterosteus aculeatus*). Intriguingly, they followed on previous tests that have shown that stickleback females based their mating preferences on olfactory cues mediated by MHC peptide ligands (Reusch et al. 2001;

Milinski et al. 2005) and now demonstrate that individual MHC diversity is involved in assortative female preference for sympatric males. These results and the similar conclusions by Knudsen et al. (2011) lend strong support for the hypothesis that parasite-mediated local adaptation may significantly contribute to diversification between populations. Van der Sluijs et al. (2011) review the evolutionary consequences of anthropogenic changes to the sensory environments of fishes. Origin and maintenance of species diversity may depend on pre-mating barriers to communication between non-related taxa. Anthropogenic disturbance of signal expression, transmission, and reception may therefore result in the loss of species boundaries. Van der Sluijs et al. (2011) further hypothesize that environmental effects on one mode of communication may trigger compensation through other modalities, and suggest to take a multimodal approach in investigating the evolutionary consequences of environmental changes on communication systems of fish. The study by Frommen et al. (2011) tackles phenotypic morphological plasticity in sticklebacks in response to odour of potential predators. Sticklebacks were able to distinguish between predatory and non-predatory fishes by olfactory cues alone, and only the odour of piscivores induced morphological changes. The faster growth of sticklebacks under the predator treatment also increased body asymmetries, suggesting developmental constraints. The fourth contribution related to ecological divergence (Gordeeva and Salmenkova 2011) studies evolutionary processes induced by transplantation of fish populations into novel environments. Pacific pink salmon (*Oncorhynchus gorbuscha*) have been transplanted from their native range along the Russian Pacific coast into European rivers at the White and Barents Sea. Due to the short life cycle and early reproduction after 2 years of life, pink salmon populations consist of two reproductively isolated broodlines which spawn alternately in even and odd years. The higher transplantation success of odd-year versus even-year broodlines suggested that strong biological differences between the broodlines such as spawning time or within-population genetic variability have accumulated despite relatively recent divergence (Gordeeva and Salmenkova 2011).

The studies summarized so far also elucidate some limitations of evolutionary studies on fish. Scientific inference has to be drawn mainly from patterns or small-scale experiments on processes guiding for example mating or habitat choice. To gain mechanistic understanding of evolutionary changes, however, a trans-generational perspective is needed (see Gordeeva and Salmenkova 2011). Many fish populations worldwide are heavily exploited by commercial and recreational fisheries and therefore have well-described population structure, abundant archived samples and long-term catch records (Nielsen et al. 2009). This enables, among others, direct observation of fisheries-induced evolution. In this special issue, three studies are included which cover different methodological approaches to fisheries-induced evolution: evaluation of long-term catch series, near-natural experimentation, and modelling.

Nusslé et al. (2011) used 25-year monitoring data of two sympatric populations of Alpine whitefishes to estimate fishing-induced selection differentials on growth rates. Marked declines in adult growth rates were found in response to intense fisheries, but selection differentials were stronger in the slow-growing *Coregonus albellus*, whereas the decline in adult growth rate seemed more pronounced in the fast-growing *C. fatioi*. No change in age at maturation or individual reproductive investment of females could be detected. Olsen and Moland (2011) claim that understanding strength and direction of harvest-induced selection versus natural selection in exploited fish populations is still limited, because following individuals in the wild is often complex and difficult. By a mixture of acoustic telemetry and traditional tagging, they give empirical evidence that harvesting can have a dominant influence on the fitness landscape experienced by coastal

Atlantic cod (*Gadus morhua*). Similarly, Matsumura et al. (2011) suggest that some degree of evolution through recreational fishing is inevitable, because no regulation measure can reduce all selection pressures on life-history traits induced by fishing to zero. These authors used an age-structured model on pike (*Esox lucius*) populations that accounts for the eco-evolutionary feedback from density-dependent and frequency-dependent selection. Fishing-induced evolution generally reduced fish size and yields, but each life-history trait responded differently to the introduction of specific harvest regulations. Accordingly, no-take reserves similar to marine fisheries have to be established also in areas intensively exploited by freshwater fisheries.

Collectively, the papers in this special issue demonstrate that fish are ideal organisms to study evolutionary responses to ecological processes and how evolutionary trade-offs, constraints and predispositions influence ecology and behaviour of populations and individuals. The studies presented here exploit the fact that fish inhabit a wide range of ecological niches and are able to specialize within astonishingly short periods of time, are often amenable to experimental manipulation, and that there are long-term data on population parameters available from commercial fishing. Furthermore, many fish populations have undergone adaptive radiations, varying from recent, incomplete speciation to cases of recently collapsed species (Joyce et al. 2005; Seehausen et al. 2008; Behm et al. 2010; Pavay et al. 2010; Hudson et al. 2011). It is therefore possible to compare the succession along the continuum of ecological speciation (Hendry 2009; Hendry et al. 2009). It is noteworthy in this context that adaptive divergence of fish populations may generate opposing effects on food webs in the preferred habitats, thus substantiating that ecological consequences of evolutionary processes are not confined to the population under study (Harmon et al. 2009; Palkovacs and Post 2009).

The dominant position of fishes as objects of studies on evolutionary ecology of animals is reflected by the number of taxon-specific publications which have appeared since 2001.

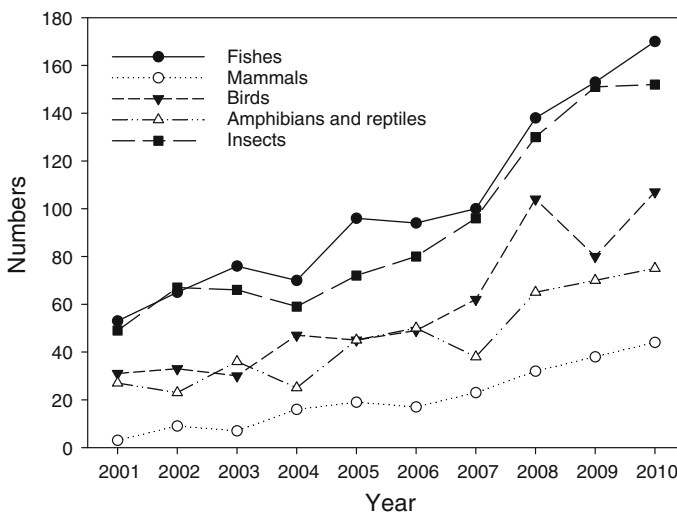


Fig. 1 Number of papers published annually between 2001 and 2010 on evolutionary ecology of fishes, mammals, birds, amphibians and reptiles, or insects. The data originate from a search in the ISI Web of Science® (www.isiknowledge.com) by using the combination (evolut* and ecol*) with either fish, bird, mammal, (amphib* or reptil*) or insect

When we searched for papers in the ISI Web of Science® (Thomson-Reuters, www.isiknowledge.com) by using the combination (evolut* and ecol*) with either fish, bird, mammal, (amphib* or reptil*) or insect for the years 2001–2010, there was a gradual increase of publications for all animal groups over recent years (Fig. 1). However, far more papers dealt with fish (total sum $n = 1,015$) than with birds ($n = 588$), amphibians and reptiles ($n = 454$) or mammals ($n = 288$). Only insects ($n = 922$) were of comparable importance as objects of evolutionary ecology research (Fig. 1).

Synthesis and future research in fish evolutionary ecology

The papers of this special issue, along with a number of other recent publications that were in part discussed at the conference, point towards three emerging aspects of evolutionary ecology that we would like to highlight here. While neither comprehensive nor representative of all innovative research topics in evolutionary ecology, these emerging topics reflect a personal preference for upcoming ideas and processes which may guide subsequent research in evolutionary ecology of fishes.

The contribution of behaviour to diversification

It has become clear that behavioural processes decisively contribute to the early stages of diversification and speciation. Fish feeding (Kahilainen et al. 2011; Knudsen et al. 2011), communication (van der Sluijs et al. 2011) and mating (Eizaguirre et al. 2011) are all involved into the formation of ecologically divergent populations. Sexual signal evolution may even outpace the ecological divergence along morphological or diet-related traits, as demonstrated for the adaptive radiation of electric fish species (*Paramormyrops* sp.) (Arnegard et al. 2010). Sexual selection can facilitate speciation under sympatric conditions, if mate choice is condition-dependent and hence ecologically and sexually selected traits diverge concomitantly (van Doorn et al. 2009).

Generally, the evolution and maintenance of divergent animal personalities (correlated behaviours or behavioural syndromes) (Schuett et al. 2010), has not yet received sufficient consideration within the framework of adaptive diversification and ecological speciation. In the context of personalities, in particular the behavioural responses to predation risk may contribute to diversification. Phenotypic variability of life histories along predation gradients has frequently been demonstrated (Walsh and Reznick 2009), and contrasting predation pressures may lead to population differentiation in personality traits (Harris et al. 2010). Phenotypic assortment of social groups is stronger under high predation risk (Croft et al. 2009a), and bold and shy guppies (*Poecilia reticulata*) differed in both their response to predators and the number of their network connections such that this positive assortment may act as an amplifier of selection towards the maintenance of cooperation (Croft et al. 2009b). Furthermore, different predator types (fish vs. predatory insects) may cause phenotypic and genetic divergence of armor in threespined sticklebacks (Marchinko 2009). Because armor expression was strongly correlated to size and size influences mate choice, predator-driven divergent selection on size may play a role in reproductive isolation and speciation in sticklebacks.

Varying respiratory and behavioural responses to confinement stress were demonstrated in eleven populations of threespined sticklebacks for which predation pressure in their native habitats differed (Bell et al. 2010). Sticklebacks from high-predation sites breathed faster and were more behaviourally responsive than fishes from low-risk sites, suggesting

that individuals can predictably adapt physiologically and behaviourally to cope with challenges in the environment. The expression of complex behaviour of ninespined sticklebacks (*Pungitius pungitius*) was found to depend on the predation level in their native habitats (Herczeg et al. 2009). Individuals from predator-free environments were quicker in feeding, bolder and more aggressive than fishes originating from high-predation sites, thus suggesting that population divergence in behaviour is mediated by predation intensity. Divergence in body shape, coupled with assortative mating for body shape, produced strong reproductive isolation between populations of mosquitofish (*Gambusia hubbsi*) inhabiting different predator regimes (Langerhans et al. 2007), thus supporting the conceptual model on condition-dependent mate choice that links ecological and sexual selection (van Doorn et al. 2009).

However, predators do not only act as direct selective agents, but can also influence the relative expression of heritable variation, for example in behavioural (personality) or morphological traits of threespined sticklebacks (Dingemanse et al. 2009b). Finally, behavioural traits of fishes most likely drive the fisheries-induced evolution of exploited populations (Uusi-Heikkilä et al. 2008).

Understudied dimensions of niche divergence

The mechanisms of ecological divergence have to be expanded beyond the commonly considered niche dimensions, which so far mainly target feeding ecology, habitat preference and the correlated morphological adaptations. A promising new route may be the explicit consideration of metabolic diversification of closely related populations (Ohlberger et al. 2008a; Pörtner et al. 2010) and the potentially correlated divergence of habitat preferences, activities and life histories (Killen et al. 2010). Genomic evidence of range-wide adaptive differentiation along habitat temperatures were found by analysing single nucleotide polymorphisms (SNP) in stocks of Atlantic cod (*Gadus morhua*) (Bradbury et al. 2010). Sympatric ciscoes (*Coregonus albula* and *C. fontanae*) presumably diverged ecologically by pelagic microhabitat segregation, guided by differing temperature optima of respiration and swimming speed and a distinctly differing final temperature preferendum (Ohlberger et al. 2008a, b). Similarly, common killifish (*Fundulus heteroclitus*) exist in two forms along the North American Atlantic coast which differ in thermal tolerance and thermal optima (Fangue et al. 2006, 2008). Temperature and metabolism interact in forming diverse groups of fishes with consistent and repeatable behaviour. A small within-day increase of temperature increased activity, boldness and aggressiveness of juvenile coral reef fishes and hence suggested that individual differences in energy metabolism may contribute to the expression of animal personalities (Biro et al. 2010). The resting metabolic rate of animals is related to the capacity to generate energy, and correlated with aggressiveness and somatic or gametic productivity, thus linking behaviour, energy metabolism and life-history ecology (Careau et al. 2008; Biro and Stamps 2010).

Another new mechanism contributing to ecological divergence may be found in the co-evolutionary arms-race between fish parasites and their hosts (Knudsen et al. 2011; Eizaguirre et al. 2011). Parasites can affect host phenotypes, for example by causing a reduction in size and shape of heads of threespined sticklebacks (Dingemanse et al. 2009a). Furthermore, parasites can increase selection against migrants between diversifying populations because migrants encounter parasites to which they are poorly adapted (Maccoll and Chapman 2010). Such changes likely have fitness consequences for hosts and may induce population divergence if parasites differ in composition or abundance between

habitats. However, the underlying mechanisms and consequences of adaptations of fishes to habitat-specific parasite assemblages are largely unknown.

The importance of behavioural processes and the understudied niche dimensions in evolutionary processes call for a more inter-disciplinary approach on evolutionary ecology of fishes. Only integrative studies on behaviour, ecology and evolution of fish individuals and populations will result in a mechanistic understanding of the expression of phenotypic variability, adaptation, ecological divergence and speciation.

Opportunities from advanced genetic analyses

A superior mechanistic understanding of adaptation and speciation will further result from genetic data that are generated by the application of rapidly developing tools, for example microarrays for high-throughput DNA and gene expression analyses, or next-generation genome or transcriptome sequencing even for non-model organisms (Stapley et al. 2010; Wolf et al. 2010; Rice and Pfennig 2010). Many long-discussed evolutionary questions such as the contributions of pre-existing or new mutations to adaptations to novel environments (Barrett and Schluter 2008), the mechanisms of convergent and parallel evolution (Arendt and Reznick 2008), and the impact of phenotypic plasticity on diversification and speciation (Aubin-Horth and Renn 2009; Pfennig et al. 2010) may soon be resolved by these new tools (Rice et al. 2011). Furthermore, whole-genome expression data will reveal new insights into the mechanisms underlying animal personalities and their evolutionary consequences (Bell and Aubin-Horth 2010). The generation of extensive genomic resources in particular for marine fishes can be expected due to the still growing worldwide demand of fish protein, which drives aquaculture activities (Canario et al. 2008).

A few examples may demonstrate the power of the new genomic technologies for resolving mechanisms of evolutionary ecology. By using microarrays, Mavarez et al. (2009) demonstrated a severe breakdown of gene expression patterns in hybrids compared with their parental relatives of anadromous and resident populations of brook charr (*Salvelinus fontinalis*). Because the disrupted genes were related to energy metabolism, immune response, osmoregulation and protection against oxidative stress, this study suggests that ecological selective pressures are the initial driving force behind disruption of gene expression in interspecific hybrids (Mavarez et al. 2009). Functional genomic studies on gill tissues using microarrays detected a common genomic signature in sockeye salmon that was associated with a 13-fold higher chance of dying during migration from the seas to the natal spawning rivers (Miller et al. 2011). Because the same genomic signature was also detected in salmon that die without spawning, the recently observed unusually high levels of mortality of Fraser River sockeye salmon may be related to physiological malfunction induced by a viral infection (Miller et al. 2011).

A high-throughput sequence-based genotyping of single-nucleotide polymorphism (SNP) markers in freshwater and oceanic populations of threespined sticklebacks revealed that replicate parallel phenotypic evolution may occur through extensive, parallel genetic evolution (Hohenlohe et al. 2010). This suggests that large panmictic oceanic populations were the source of repeated colonization of rivers by sticklebacks, resulting in phenotypically divergent freshwater populations (see also Schluter and Conte 2009). Whole transcriptome sequencing of dwarf and normal lake whitefish (*Coregonus clupeaformis*) indicated that normal whitefish overexpressed more contigs (sets of overlapping DNA segments) associated with protein synthesis while dwarf fish overexpressed more contigs related to energy metabolism, immunity and DNA replication and repair (Jeukens et al. 2010). This study thus suggests evolutionary decoupling of regulatory and coding sequences

in the adaptive divergence of fish populations. The transcriptome (de novo sequencing of cDNA) of the critically endangered European eel (*Anguilla anguilla*) has recently been analyzed to help explaining and potentially mitigating the recent dramatic decline in abundance of this commercially highly important fish species (Coppe et al. 2010).

It is intriguing to see that the detailed knowledge on the ecology and behaviour on a variety of fish populations make them ideal candidates for these upcoming in-depth genomic analyses (Stapley et al. 2010; Wolf et al. 2010; Rice et al. 2011). Accordingly, the integration of genetic data into the composite research on evolutionary ecology as described before will add the fundamental mechanistic understanding of the genomic processes of adaptation, diversification and speciation of fishes (Bernatchez et al. 2010), and hence may contribute to their conservation and management.

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