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Chapter 1

PHYLOGEOGRAPHY AND SPECIATION PROCESSES IN MARINE FISHES AND FISHES FROM LARGE FRESHWATER LAKES

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ABSTRACT

Fishes constitute about half of all known vertebrate species and have colonized nearly all available marine and freshwater habitats. The greatest diversity of fishes is found in the marine realm as well as in large (and often old) freshwater lakes such as the East African Great Lakes. Here, we compare the phylogeographic history of fishes in marine and large freshwater ecosystems, with particular emphasis on groups that underwent adaptive radiation, *i.e.* the emergence of a multitude of species from a single ancestor as a consequence of the adaptation to different ecological niches. Phylogeographic analyses are highly suited to identify and compare causal agents of speciation in rapidly diversifying groups. This is particularly true for fishes, in which distribution ranges and preferred habitat structures can be quantified in a straightforward matter.

Keywords: adaptive radiation, gene flow, cichlids, notothenioids, labrids.

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PHYLOGEOGRAPHY OF FISHES IN LARGE WATER BODIES

Since Avise *et al.* (1987) first coined the term phylogeography 23 years ago, the field has burgeoned and matured, and became a viable discipline at the intersection of population genetics, phylogenetics and biogeography (Avise 1998; 2009). The field's main concern are the principles and processes that led to contemporary geographic distributions within and between closely related species (Avise 2000). Linking micro- and macroevolutionary approaches, phylogeography has contributed greatly to species conservation, ecology and evolutionary biology. It has been integrated into the concept of 'evolutionary significant unit' (ESU) that classifies distinct populations that merit separate management and are of high priority for conservation (Ryder 1986; Moritz 1994; Crandall *et al.* 2000). Phylogeography has documented the impact of historical events on extant fauna and flora in many instances, and notably so in the case of European Pleistocene glaciations that have shaped the distribution of a wide range of European taxa (see *e.g.* Taberlet *et al.* 1998; Salzburger *et al.* 2003; Debes et al. 2008). It has also provided insights into the process of speciation (Avise 2000) when, for example the spatial simplicity and temporal certainty of volcanic archipelagos like Hawaii and the Canaries allow reconstruction of sequence and timing of speciation events (Shaw *et al.* 1996; Juan *et al.* 1998; Nepokroeff *et al.* 2003; Dimitrov *et al.* 2008; Sequeira *et al.* 2008).

A sizeable body of phylogeographic literature comes from studies conducted on teleost fishes. To some extent, this has been motivated by interest in sustained fisheries management that relies on the conservation of genetic diversity in the targeted species (Bernatchez & Wilson 1998). But fishes have also proven to be particularly informative for phylogeographic investigations. Riverine and especially lacustrine fishes inhabit island-like environments that are analoguous to volcanic archipelagos in respect of datability and spatial arrangement, and thus are similarly suitable for speciation research (Salzburger *et al.* 2005). On the other hand, marine fishes are traditionally characterized by their great diversity, their continuous and temporally stable habitat, large-scale distribution ranges, and high potential for dispersal (Palumbi 1994). Despite these differences, phylogeographic studies of marine fish species yielded important insights into population structures and their causes, the origin of marine diversity and the impact of historic events (Muss *et al.* 2001; Lourie & Vincent 2004; Rocha *et al.* 2007; Rocha *et al.* 2008). It has been shown that Pleistocene glaciations left their mark even in tropical marine settings (due to lowered sea levels; Lourie & Vincent 2004) and the phylogeography of marine species occurring on both sides of the Isthmus of Panama highlights the impact of plate tectonics on speciation over longer time scales (reviewed by Lessios 1998). Similarly, recolonization of the Mediterranean following the reopening of the Straight of Gibraltar 5.2 million years ago (MYA) (Hsü *et al.* 1973; 1977) led to a multitude of cladogenesis events that could be recovered by means of phylogeography (Carreras-Carbonell *et al.* 2005; Paternello *et al.* 2007). Furthermore, comparative phylogeography provides an adequate tool to resolve the relative impact of the many distinct life histories of marine fishes to the distributions of populations and species (Dawson *et al.* 2006). The physical setting of marine habitats also allows conclusions about these traits to be corroborated by incorporation of oceanographic data into phylogeographic analyses, *e.g.* by comparison of gene flow estimates and current speeds (Matschiner *et al.* 2009).

Thus, riverine, lacustrine, as well as marine fishes provide valuable systems for phylogeographic studies. Here, we compare the phylogeographic history of and patterns of speciation in fishes in marine and large freshwater ecosystems, with particular emphasis on groups that underwent adaptive radiation. We also present a literature review, in which we map the geographic patterns of gene flow in fish species from various taxonomic groups living in diverse environments.

THE (PHYLO-)GEOGRAPHY OF SPECIATION

One of the most hotly debated questions in speciation is certainly its geography, and, in particular, whether geographic isolation is required for new biological entities to emerge (Coyne & Orr 2004; Gavrilets 2004). Clearly, speciation can only occur via the evolution of reproductive isolation between diverging lineages. For a long time allopatric speciation[1] has been advanced as major – or even exclusive – mode of speciation (Mayr 1942; Mayr 1963). This is somewhat surprising, given that Darwin himself considered all three modes of speciation plausible (see *e.g.* Coyne & Orr 2004): allopatric[1], sympatric[2], and parapatric[3]. Since sympatric and parapatric speciation has been backed-up with theoretical and empirical evidence over the last two decades (Schliewen *et al.* 1994; Dieckmann & Doebeli 1999; Higashi *et al.* 1999; Kondrashov & Kondrashov 1999; Barluenga *et al.* 2006; Gavrilets *et al.* 2007), the debate has now shifted towards the relative importance of each of these three modes of speciation in nature.

The three possible modes of speciation explicitly impart information about geography, individual migration and gene flow. In allopatric speciation, there is absolutely no migration of individuals between the (isolated) geographic areas occupied by the speciating sub-populations; no gene flow is possible. In sympatric speciation, there is but one place, and all individuals of the speciating entities live there. Thus, there is maximum migration of individuals between the (overlapping) distribution ranges of the diverging sub-populations. This does not mean, however, that individuals belonging to distinct entities interbreed (they may do so occasionally). It simply means that individuals migrate freely in space. In parapatric speciation, a certain degree of migration occurs between the distribution ranges of the speciating sub-populations (Gavrilets 2004), and in this case interbreeding and hybrid zones are an inert feature (see *e.g.* Wu 2001; Gavrilets 2004).

There is thus an obvious and strong link between the study of speciation and phylogeography: Phylogeography provides the concepts and tools to characterize past and ongoing gene flow – and, hence, migration – in the context of geography (see *e.g.* Avise 2009). Intentionally or not intentionally, most speciation research has thus relied on and greatly benefited from phylogeography. And whenever it is necessary to explicitly interlink gene flow and distribution range – for example when testing for sympatric speciation –

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[1] *Allopatric speciation* describes the situation that there is complete geographic isolation between the speciating entities.

[2] *Sympatric speciation* can best be defined as the emergence of novel species from a population in which mating is random with respect to the birthplace of the mating partners (Gavrilets 2004).

[3] *Parapatric speciation* is everything in between complete geographic isolation and, hence, no migration between the diverging populations (allopatry) and full sympatry; it can also be described as speciation with gene flow (Wu 2001).

phylogeography is the best way to do so (see *e.g.* Barluenga *et al.* 2006; Savolainen *et al.* 2006).

MARINE *VERSUS* LACUSTRINE ADAPTIVE RADIATIONS IN FISHES

Adaptive radiation is a process in which many species evolve in a short period of time by either allopatric, sympatric or parapatric speciation. It is the rapid proliferation of an ecologically and morphologically differentiated species assemblage from one ancestral species as a consequence of the adaptation to various ecological niches (Schluter 2000) – a process that is thought to have shaped much of the diversity of life. According to Schluter (2000), adaptive radiations can be detected by four main criteria: (*i*) common ancestry of the diversifying clade; (*ii*) a correlation between morphological or physiological traits of divergent lineages and their respective environments; (*iii*) evidence for the actual utility of these traits in their environments; and (*iv*) the rapid evolution of reproductive isolation between individuals of the divergent lineages. Often – but not always – adaptive radiations occur after the colonization of a new habitat or the evolution of evolutionary 'key innovations' (Gavrilets & Vose 2005). As a consequence of the rapid cladogenesis at the onset of an adaptive radiation, phylogenies of the radiating groups are typically bottom-heavy (Gavrilets & Vose 2005) and non-bifurcating (Sturmbauer *et al.* 2003). There are not many adaptive radiations, though, for which the fulfillment of all four criteria and bottom-heavy phylogenies has been fully demonstrated.

The most famous textbook examples of adaptive radiations are the Darwin's finches on the Galapagos archipelago (see *e.g.* Grant & Grant 2002; Grant & Grant 2006), the Caribbean *Anoles* lizards (see *e.g.* Losos *et al.* 1998), and the species flocks of cichlid fishes in the Great Lakes of East Africa (Box 1). With an estimated number of at least 1,500 species, the assemblages of cichlid fishes in lakes Victoria, Malawi and Tanganyika constitute the most diverse and species-rich adaptive radiations known (Seehausen 2006; Salzburger 2009). There are, however, at least 20 more lacustrine adaptive radiations in cichlids in Africa (Seehausen 2006); and cichlid adaptive radiations are also known from outside the African continent, *e.g.*, in the Great Lakes of Nicaragua and some smaller crater lakes nearby (Barluenga & Meyer 2004; Barluenga *et al.* 2006). Why cichlid fishes are obviously prone for adaptive radiation and explosive speciation is still under debate. It seems plausible, though, that their evolutionary success rests on a unique interaction of external factors such as habitat structure and ecological opportunity and intrinsic characteristics in form of life-history traits and evolutionary key innovations like a highly adaptable feeding apparatus (Salzburger 2009).

Adaptive radiations in teleost fishes are, in general, quite common in freshwater systems: Three-spined sticklebacks (*Gasterosteus aculeatus*), for example, have repeatedly radiated into benthic and limnetic forms from ancestral marine ecotypes in post-glacial lakes (Schluter & McPhail 1992); lake whitefish (*Coregonus* spp.) have undergone adaptive radiations in post-glacial lakes, too, throughout their distribution range in the Northern hemisphere (Bernatchez *et al.* 1999; Ostbye *et al.* 2005; Vonlanthen *et al.* 2009); in the Malili lake system in Sulawesi, several species of sailfin silversides (*Telmatherina* spp.) have emerged via adaptive radiation (Herder *et al.* 2006; Roy *et al.* 2007a; Roy *et al.* 2007b); adaptive radiations have also been proposed in African weakly electric fish (*Campylomormyrus* spp.) (Feulner *et al.* 2007), in barbs (*Labeobarbus* spp.) from Lake Tana in Ethiopia (de Graaf *et al.* 2008), in cyprinids from Philippine Lake Lanao (Kornfield & Carpenter 1984), and in cyprinodontids (*Orestias* spp.) from Lake Titicaca in South America (Parenti 1984).

The situation is different in the marine realm, where much fewer cases of adaptive radiations have been described (see *e.g.* Rüber & Zardoya 2005). One of the groups that fulfills all four criteria of an adaptive radiation are the notothenioid fishes that are mainly found in Antarctic waters (Eastman 2005) (Box 2). Several evolutionary key-innovations and adaptiations have been identified (in notothenioids and subgroups thereof) that allow them to cope with the harsh environmental conditions in the Southern Ocean, such as the evolution of antifreeze glycoproteins and the losses of hemoglobin, of parts of the mitochondrial respiratory chain and of the heat-shock response system (Chen *et al*. 1997; di Prisco *et al*. 2002; Papetti *et al*. 2007a; Hofmann *et al.* 2000). However, the radiation of the whole Antarctic clade does not exhibit the bottom-heavy phylogeny (*sensu* Gavrilets & Vose 2005) theoretically expected in adaptive radiations. Instead, the full notothenioid species richness of about 130 species is attained through at least three secondary radiations – those of the artedidraconid genus *Pogonophryne*, the nototheniid subfamily *Trematominae* and the nototheniid genus *Patagonotothen* (Eastman 2005; Sanchez *et al.* 2007; Near & Cheng 2008).

Other radiations in marine fishes are less well documented than the notothenioid one and it remains to be proven whether some of these radiations are 'adaptive' after all. A second teleost radiation may have occurred in the Antarctic region. The deeper parts of the Antarctic shelf are inhabited by 64 species of the scorpaeniform family Liparidae that probably represent a secondary radiation within a larger liparid diversification, centered mainly in the North Pacific region (Eastman & Clarke 1998). The colorful parrotfishes (Scaridae), unambiguously shown to be a specialized lineage deeply nested within the family Labridae (Bellwood 1994, Westneat & Alfaro 2005), inhabit the coral reefs and seagrass beds of tropical waters. Its roughly 90 species have adapted to a variety of habitats as well as social and mating strategies in the course of a radiation that presumably started around 14 MYA in the Tethys Sea (Streelman *et al.* 2002). The overall about 600 labrid species might as well represent an adaptive radiation (Box 3), and it has been argued that – just as in cichlid fishes – a highly adaptable pharyngeal jaw apparatus might have contributed as evolutionary key innovation in that group triggering their radiation (Westneat & Alfaro 2005; Mabuchi *et al.* 2007). Reef-associated gobies, such as the American seven-spined gobies (Gobioseomatini) or the Neotropical reef gobies (*Elacatinus* spp.) apparently underwent adaptive radiations, too (Rüber *et al.* 2003; Taylor & Hellberg 2005). Recently, Puebla and coworkers (Puebla *et al.* 2007; Puebla *et al.* 2008) have highlighted an example of a marine adaptive radiation in its very first stages, once again in colorful coral reef fishes, the hamlets (genus *Hypoplectrus*, family Serranidae). These 13 closely related predatory fish species are widely distributed in the Caribbean Sea.

It is not entirely obvious why adaptive radiation should be less frequent in marine fishes compared to those in (large) freshwater lakes. One reason why there are fewer cases reported in marine fishes might be that adaptive radiations are simply more apparent in geologically young and geographically well-defined areas (Salzburger 2008), and, hence, more easy to investigate. Indeed, the best candidates for adaptive radiations in marine fishes occurred in geographically separated areas such as the Antarctic continent (notothenioids) or the

Caribbean Sea (hamlets). Older radiations, especially in tropical marine perciform families like wrasses, damselfishes, butterflyfishes, angelfishes as well as seabreams and others, date back much longer in time and might also be camouflaged by subsequent geographical separation through climatically and geologically induced range shifts or local extinctions.

THE GEOGRAPHIC SCALE OF GENE FLOW IN FISHES

Because of several reasons, fishes are an ideal group for phylogeographic research: their living space is strictly bordered by migration barriers (*e.g.* land, waterfalls, open water), their habitats are relatively easy to characterize, migration can only follow certain routes (*e.g.* ocean currents, coastlines, rivers), life-history traits (*e.g.* vagility, generation time, number of offspring) are often known, genetic tools are available, *etc*. Thus, it does not come to any surprise that a whole body of literature exists with respect to the phylogeography of various species of fish. For similar reasons, fishes are excellent models for speciation and adaptive radiation research (see *e.g.* Kocher 2004; Rüber & Zardoya 2005; Seehausen 2006; Rocha & Bowen 2008; Salzburger 2009).

Migration, gene flow and genetic differentiation are crucial parameters in both phylogeography and speciation (see above). In order to compare geographic distances over which genetic differentiation takes place in different environments and different groups of fishes, we conducted a literature review and focused on phylogeographic and population genetic studies according to the following criteria: (*i*) either DNA sequences or microsatellite loci were used as molecular markers, (*ii*) sample sizes and sampling locations were specified precisely, (*iii*) pairwise *F*-statistics or similar measures were reported, (*iv*) sequential Bonferroni correction for multiple tests (Rice 1989) or a false discovery rate (Benjamini & Hochberg 1995) was applied to pairwise comparisons, or *p*-values were reported and enabled us to conduct Bonferroni error correction. We ignored studies on populations of unresolved species status, and those that include artificially introduced or cultured populations, as well as studies investigating populations separated by artificial barriers such as river dams. Riverine populations were included only if they were sampled from the same watershed. For every study, we measured both the shortest water connection over which significant genetic differentiation was found (d_{min_s}) and the longest water connection over which no significant gene flow could be detected (d_{max_ns}). All geographic distances were measured using Google Earth®. Exact sampling locations were rarely given for anadromous species from different river systems. In these cases, the distance between river estuaries was taken. We particularly focused on three groups of perciform fishes that underwent adaptive radiations in three distinct environments: cichlids (lacustrine), labrids (tropical to temperate marine), and notothenioids (polar marine).

We based our comparison on 81 articles (marked with * in the References) investigating the population genetic stucture of 114 fish species in environments as diverse as the Arctic and the Great Barrier Reef, the Amazon River and the 34 km long Atsuta River in Japan. A number of species was investigated in more than one study or with both nucleotide and microsatellite markers, so that we ended up with 130 measurements of d_{min_s} and/or d_{max_ns}. In 37 cases, no significant genetic differentiation was found between investigated populations, while all pairwise comparisons were significant in 25 out of the 130 cases. In the most extreme cases, significant genetic differentiation was found between samples taken at the same location, but in different years (d_{min_s} = 0 km; Zane *et al.* 2006; Lin *et al.* 2008a; Hepburn *et al.* 2009), or no comparison was significant despite a global sampling scheme (d_{max_ns} = 16,309 km; Horne *et al.* 2008).

The shortest geographic distances, over which significant genetic differentiation was found in different taxonomic groups and environments are visualized in Figure 1. Naturally, these measures may depend on parameters such as study design, sample size and number of markers employed. In Figure 2, we plotted d_{min_s} against the sample size of the respective study. Indeed, the result suggests a negative correlation between both values. However, as the average sample sizes were comparable between studies in different fish taxa and environments (with the exception of anadromous fishes: N = 825; others: N = 130-333), the overall picture shown in Figure 1 should not be influenced by the different study practices applied by the different researcher groups.

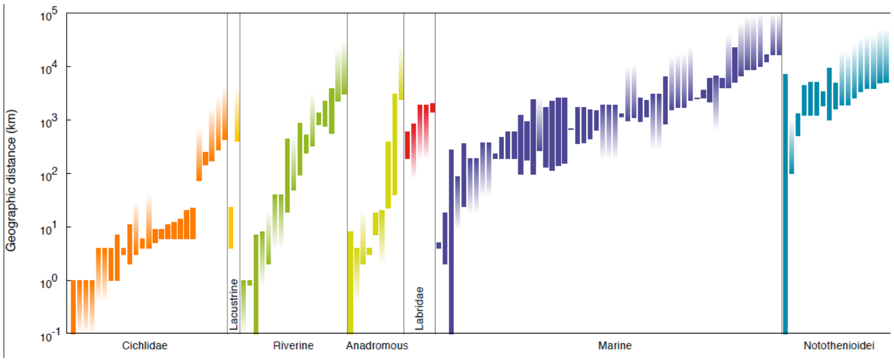

Figure 1. The geographic scale of gene flow in fishes. Shortest geographic distances over which significant genetic population differentiation have been found in different taxonomic groups and environments. Each bar represents one analysis of population differentiation. Bars are drawn between the shortest distance, over which significant differentiation has been found (d_{min_s}), and the longest distance, over which no significant differentiation could be detected (d_{max_ns}). A downward gradient symbolizes that all pairwise comparisons were significant. In these cases, the gradient's top end represents d_{min_s}. This visualizes that significant differentiation could be expected at even shorter, untested distances. Similarly, an upward gradient symbolizes that no pairwise comparison was significant, and that significant differentiation can be expected only at distances greater than those tested (d_{max_ns} is the gradients lower end). All distances were measured as the shortest water connections between fish populations.

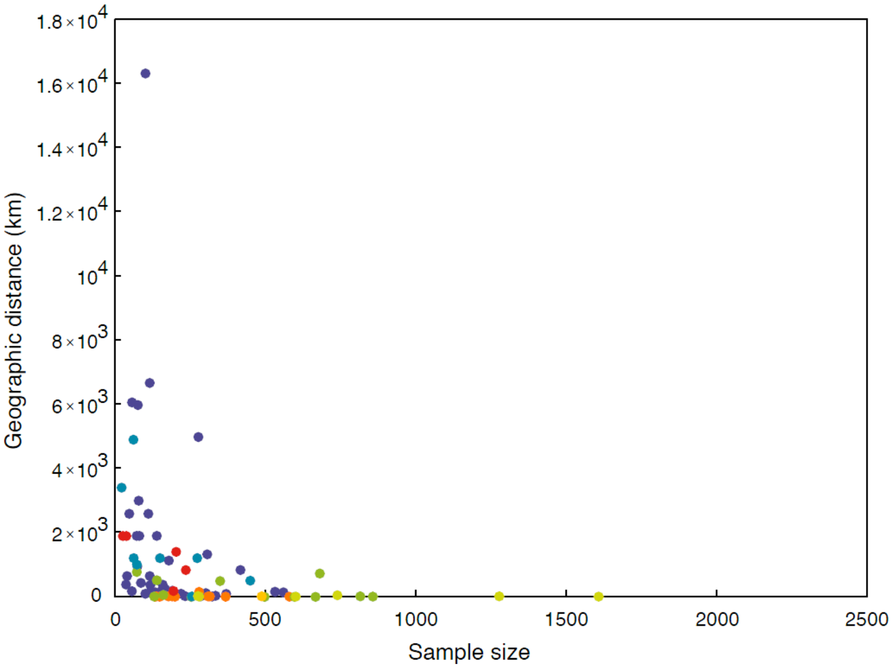

Figure 2. Sample size effects in phylogeographic studies in fishes. The shortest geographic distance over which significant differentiation has been detected plotted against sample size. Color code as in Figure 1.

Lacustrine Fishes

Differentiation over short geographic distances on the order of 10 km and below is commonly found in rock-dwelling cichlids of the East African Great Lakes, and it has been speculated whether their tendency to philopatry and the resulting barriers to gene flow has enabled local adaptation, speciation, and their impressive adaptive radiation (Rico & Turner 2002; Pereyra *et al.* 2004). However, the cichlid radiations also include a number of pelagic species that show genetic homogeneity over hundreds of kilometers, and thus would contradict this hypothesis (see the five bars at the right end of the Cichlidae column in Fig. 1) (Shaw *et al.* 2000; Taylor & Verheyen 2001). We found two studies on non-cichlid lacustrine fishes that matched our criteria: Sailfin silversides of Lake Matano, Indonesia, show significant differentiation at small geographic distances (Walter *et al.* 2009), while large-scale gene flow was observed in the little Baikal oilfish in Lake Baikal, Russia (Teterina *et al.* 2005).

Riverine and Anadromous Fishes

Very variable patterns were found in riverine and anadromous fish species. In the case of the riverine fishes, it appears that river size influences rates of gene flow between populations: Genetic differentiation over short distances was found repeatedly in small river systems such as the Caroni Drainage, Trinidad and Tobago (d_{min_s} = 1 km, all comparisons being significant; Barson *et al.* 2009), the Amor de Cosmos watershed on Vancouver Island, Canada (d_{min_s}, d_{max_ns} = 1 km; Caldera & Bolnick 2008), and the Novoselka River basin, Sakhalin, Russia (d_{min_s} = 1 km, d_{max_ns} = 7 km; Osinov & Gordeeva 2008). On the other hand, population genetic assessments of fishes of the Amazon River frequently fail to detect significant population structure over the entire sampling area ($\mathrm{d}_{\mathrm{max\_ns}}$ > 2000 km; Batista & Alves-Gomes 2006; Santos *et al.* 2007).

Marine Fishes

In general, marine fishes show great variability in their patterns of differentiation: While reef fishes with low dispersal abilities may exhibit significant population structure at less than 10 km (Miller-Sims *et al.* 2008; Bay *et al.* 2008), most marine fishes display differentiation only at distances of hundreds to thousands of kilometers; no genetic structuring even at a global scale has been observed in lemon sharks (Schultz *et al.* 2008) and two surgeonfishes (Horne *et al.* 2008). Fishes of the family Labridae show comparable patterns of differentiation between the different species. Significant population structure was found between 187 and 1898 km. Fishes of the perciform suborder Notothenioidei show little genetic structuring even compared to other marine fish taxa. One exception aside (significant structure between year-classes sampled at the same location; Zane *et al.* 2006), significant genetic differentiation has been found only over several hundreds or thousands of kilometers, or not at all, as is the case for the majority of studies included in our survey. As the life histories of most notothenioids include long pelagic larval stages of up to one and a half years (Kock & Kellermann 1991; La Mesa & Ashford 2008), it has been speculated that strong oceanic currents, and in particular the Antarctic Circumpolar Current (ACC) may be responsible for gene flow in form of larval dispersal (Zane *et al.* 2006; Jones *et al.* 2008). Using a multidisciplinary approach including oceanographic data and simulations using the isolation-with-migration (IM) model (Hey & Nielsen 2007) to investigate directionality of gene flow in the notothenioid fish *Gobionotothen gibberifrons*, Matschiner *et al.* (2009) indeed found highly asymmetric migration rates between the Antarctic Peninsula and islands of the Scotia Ridge, following the direction of the ACC. As gene flow caused by long-distance migration of adult individuals would be expected to result in roughly symmetric migration rates, this finding corroborates the hypothesis that larval dispersal precludes genetic differentiation in Antarctic waters even across large geographic distances.

THREE ADAPTIVELY RADIATING PERCIFORM GROUPS

At least one in two vertebrate species is a fish and within the fishes at least one third (and more than 10,000 species) belongs to the order Perciformes, making it the largest order of vertebrates. The Perciformes itself is comprised of about 160 families and more than 1500 genera and they dominate vertebrate life in the ocean and in tropical and subtropical freshwaters (Nelson 2006). Much of the diversity of perciforms has arisen through adaptive radiations, of which the ones of the cichlid fishes are the most impressive. Marine (adaptive) radiations within the Perciformes are those of the notothenioids, of the labrids, the gobies, and the hamlets (Eastman 2005; Westneat & Alfaro 2005; Rüber *et al.* 2003; Puebla *et al.* 2008). Massive bursts of diversification ('explosive speciation') have repeatedly been reported for East African cichlid fishes (*e.g.* McCune 1997; Seehausen 2002; Verheyen *et al.* 2003). In marine fishes, elevated rates of cladogenesis were reported – among others – for *Sebastes* rockfishes, the notothenioid subfamily Trematominae, American seven-spined gobies and sparids (Rüber & Zardoya 2005).

Here, we focus on three groups of Perciformes that apparently underwent adaptive radiations and episodes of explosive speciation in different environments (Eastman & Clarke 1998; Eastman 2005; Seehausen 2006; Mabuchi *et al.* 2007): the cichlids of the tropical Great Lakes in East Africa (Box 1), the notothenioids of the polar marine waters of Antarctica (Box 2), and the labrids of the tropical and subtropical marine waters (Box 3). The adaptive radiations of all three groups have been associated with evolutionary key-innovations (Liem 1973; Chen *et al.* 1997; Hulsey 2006; Mabuchi *et al.* 2007), they all evolved a spectacular diversity of body morphologies and – in the case of cichlids and labrids – color morphs, and members of all three groups dominate their respective fauna.

Phylogeographic and population genetic studies in the three groups cichlids, notothenioids, and labrids reveal substantial differences with respect to the geographic distances over which gene flow could be detected (Figure 1). While in most cichlid species population structure could be detected over small geographic ranges of below or around 10 km, labrids and – with one exception – notothenioids show gene flow over large geographic distances. The latter two groups lie well in the range of other marine fishes, just as a few pelagic cichlid species do (note that the upper geographic limits in these cichlid species is restricted by lake size). This discrepancy between gene flow on a circumantarctic scale in notothenioids and large distances in labrids and the fine-scale genetic structuring in cichlids of the East African Lakes seems puzzling, given that all these clades underwent adaptive radiations in their respective environments, and philopatry has often been proposed as one of the key agents behind local adaptation and, consequently, adaptive radiation (Bouton *et al.* 1999; Rico & Turner 2002; Rico *et al.* 2003; Pereyra *et al.* 2004; Taylor & Hellberg 2005; Gavrilets *et al.* 2007).

Gene flow is generally expected to retard speciation by breaking linkage between genes for local adaptation and those for reproductive isolation (Coyne & Orr 2004). On the other hand, recent theoretical work as well as empirical research (Gavrilets & Vose 2005; Seehausen 2006; Garant *et al.* 2007) has shown that gene flow between populations does not necessarily prevent local adaptation. To the contrary, it can facilitate the spread of beneficial mutations and thus support adaptation under certain circumstances. In the context of adaptive radiation, the individual-based stochastic model of Gavrilets & Vose (2005) predicted that divergence can be maintained for very long periods despite substantial amounts of gene flow, which would lead to a 'porous' genome with low to non-existing differentiation in neutral markers, but divergence at locally selected loci. Evidence for porous genomes has been found in the *Hypoplectrus* complex of coral reef fishes that are supposed to represent an adaptive radiation in its very first stages (Puebla *et al.* 2008).

PHYLOGEOGRAPHY AND SPECIATION IN MARINE *VERSUS* LACUSTRINE FISHES

So what is it that could explain the difference between marine fishes with gene flow over large geographic distances and fishes from large freshwater lakes with often highly structured populations?

Habitat discontinuities, which have been suggested as main reason why rock-dwelling cichlid populations are so structured (Arnegard *et al.* 1999; Rico & Turner 2002; Pereyra *et al.* 2004; Duftner *et al.* 2006; Sefc *et al.* 2007), can only partly explain these differences. Marine reefs are highly fragmented, too. Still, gene flow in reef associated fishes can be observed over large geographic distances, *e.g.* between the West and East Atlantic (Floeter *et al.* 2008; Rocha *et al.* 2008) or between Caribbean islands over hundreds of kilometers (Puebla *et al.* 2008). Habitats of benthic notothenioids are disrupted by iceberg scours (Brenner *et al.* 2001) and open water between island shelves, while the habitat of a limited number of pelagic notothenioids may be assumed continuous over thousands of kilometers (Zane *et al.* 2006). Nevertheless, pelagic and benthic notothenioids alike apparently maintain gene flow over these large distances (Figure 1) (Matschiner *et al.* 2009).

Another extrinsic factor that might explain the observed differences in population structure is *habitat stability*. Large freshwater lakes are very young compared to marine habitats. Lake Tanganyika, for example, the oldest of the East African Great Lakes and second oldest lake in the world, has a maximum age of 12 million years (MY) (Cohen *et al.* 1997); Lakes Malawi and Victoria are considerably younger. More importantly, the lakes have repeatedly undergone dramatic water-level fluctuations of up to several hundred meters. In the case of Lake Victoria, this is equivalent to a complete desiccation, but fish diversity may have survived in tributaries and satellite lakes (Johnson *et al.* 1996; Cohen *et al.* 1997; Mwanja *et al.* 2001; Verheyen *et al.* 2003; Stager & Johnson 2008). It has been argued that these cyclic changes leading to admixis, hybridization, fragmentation of populations, and small founder populations, contributed to the species-richness in the East African lakes (Rossiter 1995; Kornfield & Smith 2000; Sturmbauer *et al.* 2001). It is less apparent, though, how these lake-level fluctuations could account for the structuring in present cichlid populations. Dramatic changes in the environment also characterize the marine habitat of Antarctic notothenioids. During the last two MY, the Antarctic ice sheet has periodically advanced and retreated with each glacial cycle. Presumably it has extended all the way to the shelf edge in glacial maxima (Thatje *et al*. 2005), 'bulldozing the surviving fauna to the deep continental margin' (Barnes & Conlan 2007). Naturally, the associated loss of benthic habitat must place serious constraints on demersal fish communities. There is evidence for at least some refuges in form of ice-free shelf areas (Barnes & Conlan 2007) that could provide analogues to satellite lakes of Lake Victoria during desiccation periods.

The temporal scale of significant and drastic environmental change is clearly different for wrasses and other tropical marine reef fishes and reaches back as far as the Eocene. The split of the most species-rich wrasse lineage, the Julidini, covering about one-third of overall labrid diversity was recently calculated of an age of 36 to 38 MY (Kazancioglu *et al.* 2009) supporting the hypothesis of their Tethyan origin and Indo-Pacific ancestral distribution (Westneat & Alfaro 2005). These estimates imply that by the time the julidine lineage originated, the Antarctic Circumpolar Current was already established, which disrupted the connection between higher and lower latitudes, and restricted the movement of tropical lineages to the Tethys (Bellwood & Wainwright 2002). A series of diversification events within the Julidini leading to an early burst of diversification and the evolution of the majority of extant julidine lineages nicely coincides with a period of increased diversification and fragmentation of coral reefs, and extensive development of reef communities in the Tethys and the Caribbean (Veron 1995) between 15 to 30 MY (Kazancioglu *et al.* 2009). Habitat fragmentation culminated in the middle Miocene with its rapidly changing paleobiogeographical conditions and strong tectonic activity (Rögl, 1999) that resulted in the final closure of seaway between the Mediterranean and the Indian Ocean some 14 MYA. Hanel *et al.* (2002) correlated the following succession of the Mediterranean with the radiation of the wrasse tribe Labrini, endemic to the northern Atlantic and found striking congruence.

Among the intrinsic (biotic) differences between marine fishes and fishes from large freshwater lakes is the *degree of specialization*. While most lacustrine East African cichlid species are ecologically highly specialized, the majority of marine fishes are not (at least not to the degree observed in cichlids). Rocha & Bowen (2008) attest that most reef fishes are ‘neither widely distributed generalists nor ecological specialists’. Clearly, specialization limits gene flow by lowering survival rates and reproductive success of migrants. The question remains whether the much greater degree of specialization is a reason for or the outcome of the limited levels of gene flow between cichlid populations.

Another difference between marine fishes and cichlids is the *breeding behavior*. It is interesting though that in all three groups that underwent adaptive radiations, cichlids, notothenioids and labrids, a certain degree of brood care occurs. The cichlids are famous for their various systems and strategies of brood care behavior ranging from substrate spawning in nests and under custody of the parents to various levels of mouthbrooding (Goodwin *et al.* 1998; Barlow 2000).

Prolonged incubation and pelagic larval duration are common features of most Antarctic notothenioids (Kock & Kellermann 1991, Loeb *et al.* 1993). For example, hatching of larvae of the naked dragonfish *Gymnodraco acuticeps* occurs only about 10 months post-fertilization (Evans *et al.* 2005), while the Scotia Sea icefish *Chaenocephalus aceratus* undergoes an extensive pelagic phase as long as 1.5 years (La Mesa & Ashford 2008). Brood care of demersal eggs has been reported for a number of species and even egg carrying behavior has been observed in one icefish species (*Chionobathyscus dewitti*; Kock *et al.* 2006). However, other nototheniod fishes are open spawners that release their eggs in the open water column, or produce demersal eggs that become pelagic towards the end of their development (Kock 2005; Kellermann 1991). Pelagic eggs and larvae are prone to off-shelf advection and dispersal with strong oceanic currents such as the ACC. While active larval behavior, especially towards the end of the larval phase, may counteract dispersal in many cases (White 1998; Leis 2006), pelagic eggs and larvae have been found hundreds of kilometers away from suitable shelf habitat (Kellermann 1991; Loeb *et al.* 1993). Widespread larval dispersal is further suggested by the fact that only nototheniids and channichthyids with particularly long pelagic larval durations occur at the isolated island of Bouvetøya (Jones *et al.* 2008).

Within the percomorpha, the family Labridae can be considered exceptional in terms of diversity of social and reproductive systems. Most wrasses are sequential hermaphrodites, with a transformation from female to male state being the normal occurrence. The causes and pathways of the evolution of hermphroditism, regularly found in percomorph marine fishes, as reproductive style have been and are still subject of debate (Atz 1964, Smith 1967, 1975, Ghiselin 1969, Reinboth 1970, Policansky 1982). One clear advantage should be to maximize lifetime reproductive potential (Williams 1966) and hence individual fitness (*sensu* Stearns 1976). However, courtship, spawning, and sex change can be quite varied with mating systems in wrasses including haremic mating groups, promiscuity, lek-like behavior leading to group spawning, and facultative monogamy (pair spawning) (Donaldson, 1995). A change in sex is often associated with a change in color pattern. Broadcast spawning is a general rule in the Labridae, with most species being characterized by planktonic eggs and larvae and therefore a lack of any kind of brood care behavior, a pattern typical for the majority of marine fish species. In contrast, brood care is well developed in the comparatively small wrasse tribe Labrini (Hanel *et al.* 2002). Labrine wrasses show a variety of different brood care strategies, representing evolutionary succession from simple formation of spawning cavities up to the construction of complex nests associated with extensive egg care performed by territorial males and supported by one to several “helpers”. Nevertheless, the effect of different brood care strategies on population size and structure as well as on phylogeography has, to our knowledge, not yet been tested.

CONCLUSION

Over the past two decades, fishes have emerged as excellent model groups for the study of phylogeography, speciation and adaptive radiation. This is not least due to their well-defined habitats, the existence of strong migration barriers bordering their living space, their restricted possibilities for migration and dispersal, and the availability of genetic tools. Different groups of fishes vary with respect to phylogeography and population structure: An extensive literature review revealed substantial differences in the geographic distances over which gene flow was detected in various groups of fishes that inhabit diverse environments. Marine fish typically show low to non-existing gene flow over hundreds to thousands of kilometers, while populations of lacustrine fishes, such as the cichlid fishes in the East African Great Lakes, are typically highly structured. Three groups of the highly diverse perciform fishes that underwent adaptive radiations are the cichlids, the notothenioids and the labrids. They radiated in large freshwater lakes, the polar waters of Antarctica, and tropical to temperate marine environments, respectively. Speciation and diversification in all three groups has been connected to external factors such as habitat instability, and paleo-geological and paleo-climatological processes, and all three radiations have been associated with evolutionary key-innovations. Still, they differ in overall within-species phylogeography, in population structure and patterns and levels of gene flow. The marine representatives are also generally less specialized than the cichlids. Whether this is due to differences in life-history traits, such as breeding behavior, would need to be investigated.

Box 1: The adaptive radiations of cichlid fishes

The perciform family of the Cichlidae represents a group of tropical and subtropical freshwater fish that show an Gondwanian distribution with ancestral and relatively species-poor lineages in India, Sri Lanka and Madagscar and two highly diverse clades in South- and Central America and in Africa, respectively (Salzburger & Meyer 2004). The most impressive cichlid adaptive radiations have occurred in the East African Great Lakes where at least 1500 species have evolved in the last few millions to several thousands of years only (Kocher 2004; Seehausen 2006; Salzburger 2009). Various hypotheses exist with respect to the evolutionary success of this group, and it seems likely that a unique combination of intrinsic (biotic) and extrinsic (abiotic) factors have triggered their adaptive radiations (Salzburger 2009). It has long been suggested that the particular architecture of the cichlid's jaw apparatus – with a second set of jaws in the pharynx – has acted as evolutionary key innovation in the adaptive radiations cichlids (Liem 1973). The most species-rich group of cichlids, the haplochromines from East Africa, are characterized by their particular kind of maternal mouthbrooding and egg-dummies on the male anal fins, which mimic real eggs and aid to bring the females mouth close to the male's genital opening. Both maternal mouthbrooding and egg-dummies might have acted as key-innovations, too (Salzburger *et al.* 2005; Salzburger 2009). It appears that both, ecologically relevant and, hence, naturally selected traits (*e.g.* moth morphology, body shape) and sexually selected traits (*e.g.* coloration) are important during cichlid speciation (Salzburger 2009).

Possible extrinsic factors are repeatedly occurring fluctuations of the lake level and the habitat diversity found in the East African lakes (Sturmbauer 1998; Kornfield & Smith 2000; Sturmbauer *et al.* 2001). Habitat discontinuities, together with often philopatric and stenotopic behavior of many of the cichlid species, may be partly responsible for their explosive speciation in lakes Victoria, Malawi and Tanganyika (van Oppen *et al.* 1997; Rico & Turner 2002; Rico *et al.* 2003; Pereyra *et al.* 2004; Duftner *et al.* 2006; Sefc *et al.* 2007).

Number of species (estimated): 3000-5000
Distribution range: Gondwanian (India, Sri Lanka, Madagascar, Africa, South- and Central America)
Habitat: freshwater (lakes and rivers)
Key-innovations (suggested): pharyngeal jaw apparatus, egg-dummies

Box 2: The adaptive radiation of notothenioids

Fishes of the perciform suborder Notothenioidei have successfully colonized the Antarctic waters and radiated under these harsh conditions. Today, the notothenioids dominate the Antarctic continental shelf and upper slope in terms of species number (47%) and biomass (90-95%) (Eastman & Clarke, 1998). Estimates for the onset of the notothenioid radiation range between 24 (Near 2004) and 7-15 MYA (Bargelloni *et al.* 1994; Cheng *et al*. 2003). Today, eight families and at least 130 notothenioid species are known. The three basal families, Bovichtidae, Pseudaphritidae and Eleginopidae comprise 13 species, 12 of which are non-Antarctic and occur in the coastal waters of New Zealand, Australia and around the tip of South America. The five remaining families Nototheniidae, Harpagiferidae, Artedidraconidae, Bathydraconidae and Channichthyidae consist of 116 mainly Antarctic species (Eastman 2005). Typically, only the latter five families (the 'Antarctic clade') are referred to when speaking of the notothenioid radiation.

The remarkable diversification of the Notothenioidei has been accompanied by several innovations in physiology. The most general feature found in all notothenioids, but not in higher-level relatives, is a lack of swim bladders. For this reason, most notothenioids are heavier than seawater and dwell on or near the seafloor. However, several notothenioid lineages have independently colonized the water column in a trend termed pelagization (Klingenberg & Ekau 1996). The expression of heat-shock proteins (HSPs) as a response to elevated temperatures, a feature that is regarded as a universal characteristic of almost all organisms, has been found absent in the highly cold-adapted members of the Antarctic clade (Hofmann *et al.* 2000; Clark *et al.* 2008). Recently, it has been shown that members of the Antarctic clade lack the mitochondrial *ND6* gene (coding for the NADH-Dehydrogenase subunit 6) (Papetti *et al.* 2007a). All members of the most derived notothenioid family, the Channichthyidae, have lost the ability to synthesize hemoglobin (Ruud 1954; Eastman 1993), and thus represent the only vertebrates without oxygen-bearing blood pigments. While the absence of hemoglobin is due to the deletion of the β-globin subunit gene in a single deletion event (di Prisco *et al.* 2002), truncated and inactive remnants of the α-globin gene are retained in channichthyid genomes (Cocca *et al.* 1995; Near *et al.* 2006). Since the oxygen-carrying capacity of the hemoglobinless phenotype is reduced by a factor of ten, the Channichthyidae evolved compensational features such as a blood volume two to four times that of comparable teleosts, a large stroke volume and cardiac output, and relatively large diameters of arteries and capillaries (Eastman 1993).

The most remarkable innovation of notothenioids are special blood-borne antifreeze glycoproteins (AFGPs), that are present in all notothenioids of the Antarctic clade, and enable them to cope with the subzero temperatures of Antarctic waters (Cheng *et al.* 2003). There is evidence that the AFGPs evolved only once in notothenioids from a trypsinogen ancestor gene, and that this happened before the diversification of the Antarctic clade (Chen *et al.* 1997; Cheng *et al.* 2003). It is thus tempting to attribute the notothenioid radiation to the evolution of AFGPs as a key adaptation with respect to the cooling environment. It may have enabled the notothenioids to survive the temperature drop in Antarctic waters from around 20˚C to the current freezing conditions (Clarke & Johnston 1996), and to radiate while most other teleosts could not adapt to the decreasing temperatures.

Number of species: ca. 130
Distribution range: Antractic waters, South Pacific
Habitat: polar marine
Key-innovations (suggested): antifreeze glycoproteins

Box 3: The (adaptive) radiation of labrids

The perciform family Labridae is a diverse group of about 600 mostly reef-dwelling species in 82 genera that exhibit an exceptional diversity in body size, shape, coloration, feeding habits, reproductive behaviors, and life histories (Westneat 1999, Parenti & Randall 2000, Wainwright *et al.* 2004, Westneat & Alfaro 2005). Together with the parrotfishes (Scaridae) as well as the cales and weed-whitings (Odacidae), which were all shown to be deeply nested within the Labridae (Bellwood 1994, Westneat and Alfaro 2005), wrasses comprise the worldwide second largest family of marine fish.

As with many percoid families the fossil record of the Labridae extends back to the Eocene (Lower Tertiary, approx. 54 MYA) (Berg 1958; Patterson, 1993) with *†Phyllopharyngodon longipinnis* Bellwood 1990 being described from a specimen recovered from the Pesciara ("Fish Bowl") in Monte Bolca, Italy (Bellwood 1990). Being dated to topmost Ypresian or lowermost Lutetian (Benton *et al.* 1993), this results in an estimated age of about 48 to 50 MY (Luterbacher *et al.* 2004). Based on the presence of a single predorsal, a well-developed pharyngeal jaw, and the phyllodont form of the teeth found on the pharyngeal jaw, Bellwood (1990) placed the specimen with confidence among the basal wrasse clade Hypsigenyini. However, based on plate tectonics, dating of reef lineages with molecular clocks and patterns of fish otolith preservation, the overall age of the family is estimated to be anywhere between 50 and 90 MY (Bellwood & Wainwright 2002, Westneat & Alfaro 2005).

From an oceanographic point of view, this time period near the end of the Mesozoic and beginning of the Cenozoic was characterized by the continuation of the Gondwana break-up to form present-day shaped continents as well as the central role of the circum-tropical Tethys Sea connecting the Indian with the Atlantic Ocean.

Diversification of the Labridae has often been referred to as a consequence of the evolution of functional novelties in the feeding apparatus that have allowed them to occupy nearly every feeding guild in reef environments (Westneat & Alfaro 2005). Feeding habits in the group are as diverse as in cichlids, including specialized predation on gastropods, bivalves, crustaceans, fishes, coral mucous, zooplankton, ectoparasites, detritus and algae (Randall 1967, Westneat 1997). However, recent investigations point out that territorial behavior and strong sexual dichromatism, as expressed by many wrasse species, may effectively drive sexual selection and are therefore major factors for labrid diversification (Kazancioglu *et al.* 2009).

Number of species (estimated): 600
Distribution range: global
Habitat: tropical to temperate marine
Key-innovations (suggested): pharyngeal jaw apparatus

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