

The exclusive license for this PDF is limited to personal printing only. No part of this digital document may be reproduced, stored in a retrieval system or transmitted commercially in any form or by any means. The publisher has taken reasonable care in the preparation of this digital document, but makes no expressed or implied warranty of any kind and assumes no responsibility for any errors or omissions. No liability is assumed for incidental or consequential damages in connection with or arising out of information contained herein. This digital document is sold with the clear understanding that the publisher is not engaged in rendering legal, medical or any other professional services.

Chapter 1

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

Michael Matschiner¹, Reinhold Hanel^{2} and
Walter Salzburger¹*

¹Zoological Institute, University of Basel, Basel, Switzerland

²Institute of Fisheries Ecology, Johann Heinrich von Thünen-Institute,
Hamburg, Germany

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 manner.

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

* Author of correspondence. Reinhold Hanel
E-mail: reinhold.hanel@vti.bund.de

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 analogous 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 Strait 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 speciation¹ 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): allopatric¹, sympatric², and parapatric³. Since sympatric and parapatric speciation has been backed-up with theoretical and empirical evidence over the last two decades (Schlieven *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 –

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 group 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 adaptations 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 structure 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).

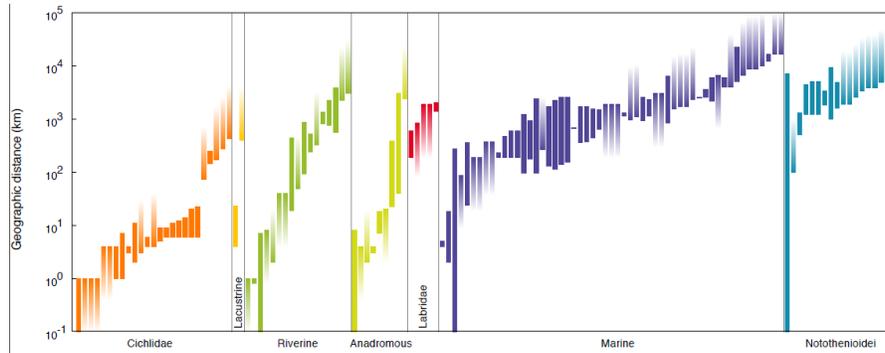


Figure 1. The geographic scale of gene flow in fishes. Shortest geographic distances over which significant genetic population differentiation have been found in different taxonomic groups and environments. Each bar represents one analysis of population differentiation. Bars are drawn between the shortest 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 gradient's lower end). All distances were measured as the shortest water connections between fish populations.

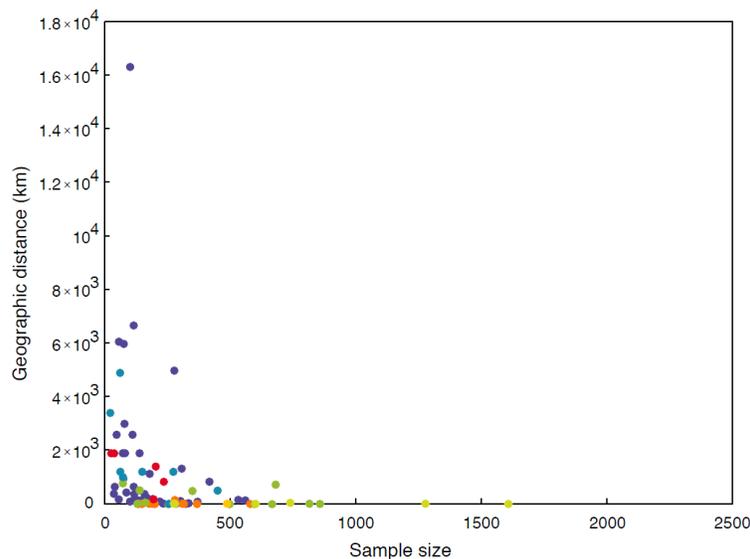


Figure 2. Sample size effects in phylogeographic studies in fishes. The shortest geographic distance over which significant differentiation has been detected plotted against sample size. Color code as in Figure 1.

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.

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 ($d_{max_{ns}} > 2000$ 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 notothenioid 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 hermaphroditism, 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 harem 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.

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 Madagascar 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: Antarctic 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 phylodont 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

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.

ACKNOWLEDGMENTS

We would like to acknowledge our respective grant sponsors, the VolkswagenStiftung to MM, the German Science Foundation (DFG) to RH, and the Swiss National Science Foundation (SNF) and the European Research Council (ERC) to WS.

REFERENCES

- *Abila R, Barluenga M, Engelken J, Meyer A, Salzburger W (2004) Population-structure and genetic diversity in a haplochromine fish cichlid of a satellite lake of Lake Victoria. *Molecular Ecology* 13 (9), 2589-2602.
- *Appleyard SA, Williams R, Ward RD (2004) Population genetic structure of Patagonian toothfish in the West Indian sector of the Southern Ocean. *CCAMLR Science* 11, 12-32.
- *Arnegard ME, Markert JA, Danley PD, Stauffer JR, Ambali AJ, Kocher TD (1999) Population structure and colour variation of the cichlid fish *Labeotropheus fuelleborni* Ahl along a recently formed archipelago of rocky habitat patches in southern Lake Malawi. *Proc R Soc Lond B Biol Sci* 266, 119-130.
- Atz JW (1964) Intersexuality in fishes. In: *Intersexuality in vertebrates including man* (eds. Marshall AJ, Armstrong CN) pp. 145-232. Academic Press, NY.
- *Aurelle D, Guillemaud T, Afonso P, Morato T, Wirtz P, Santos RS, Cancela ML (2003) Genetic study of *Coris julis* (Osteichthyes, Perciformes, Labridae) evolutionary history and dispersal abilities. *Comptes Rendus Biologies* 326, 771-785.
- Avise JC (1998) The history and purview of phylogeography: a personal reflection. *Molecular Ecology* 7, 371-379.
- Avise JC (2000) *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge, MA.
- Avise JC (2009) Phylogeography: retrospect and prospect. *Journal of Biogeography* 36, 3-15.
- Avise JC, Arnold J, Ball RM, Bermingham E, Lamb T, Neigel JE, Reeb CA, Saunders NC (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics* 18, 489-522.
- *Baerwald MR, Feyrer F, May B (2008) Distribution of genetically differentiated splittail populations during the nonspawning season. *Transactions of the American Fisheries Society* 137 (5), 1335-1345.
- Bargelloni L, Ritchie PA, Patarnello T, Battaglia B, Lambert DM, Meyer A (1994) Molecular evolution at subzero temperatures: mitochondrial and nuclear phylogenies of fishes from Antarctica (suborder Notothenioidei), and the evolution of antifreeze glycopeptides. *Molecular Biology and Evolution* 11 (6), 854-863.
- Barlow GW (2000) *The Cichlid Fishes. Nature's Grand Experiment in Evolution*. Perseus Publishing, Cambridge, MA.

- Barluenga M, Meyer A (2004) The Midas cichlid species complex: incipient sympatric speciation in Nicaraguan cichlid fishes? *Mol Ecol* 13, 2061-2076.
- Barluenga M, Stolting KN, Salzburger W, Muschick M, Meyer A (2006) Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature* 439, 719-723.
- Barnes DKA, Conlan KE (2007) Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 362 (1477), 11-38.
- *Barroso RM, Hilsdorf AWS, Modeira HLM, Cabello PH, Traub-Cseko YM (2005) Genetic diversity of wild and cultured populations of *Brycon opalinus* (Cuvier, 1819) (Characiforme, Characidae, Bryconinae) using microsatellites. *Aquaculture* 247, 51-65.
- *Barson NJ, Cable J, van Oosterhout C (2009) Population genetic analysis of microsatellite variation of guppies (*Poecilia reticulata*) in Trinidad and Tobago: evidence for a dynamic source-sink metapopulation structure, founder events and population bottlenecks. *Journal of Evolutionary Biology* 22 (3), 485-497.
- *Batista JS, Alves-Gomes JA (2006) Phylogeography of *Brachyplatystoma rousseauxii* (Siluriformes - Pimelodidae) in the Amazon Basin offers preliminary evidence for the first case of "homing" for an Amazonian migratory catfish. *Genetics and Molecular Research* 5 (4), 723-740.
- *Bay LK, Caley MJM, Crozier RH (2008) Meta-population structure in a coral reef fish demonstrated by genetic data on patterns of migration, extinction and re-colonisation. *BMC Evolutionary Biology* 8 (1), 248.
- Bellwood DR (1990) A new fossil fish *Phyllopharyngodon longipinnis* gen. et sp. nov. (family Labridae) from the Eocene, Monte Bolca, Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 6, 149-160.
- Bellwood DR (1994) A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidei), with a revision of genera. *Records of the Australian Museum Supplement* 20, 1-86.
- Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. Sale PF), pp. 5-32. Academic Press San Diego, CA.
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Society B: Methodological* 57 (1), 289-300.
- Benton MJ (1993) *The Fossil record* 2. Chapman & Hall, London, UK.
- Berg LS (1958) *System der rezenten und fossilen Fischartigen und Fische*. VEB Verlag der Wissenschaften, Berlin.
- Bernatchez L, Chouinard A, Guoqing L (1999) Integrating molecular genetics and ecology in studies of adaptive radiation: whitefish, *Coregonus* sp., as a case study. *Biological Journal of the Linnean Society* 68, 173-194.
- Bernatchez L, Wilson CC (1998) Comparative phylogeography of Nearctic and Palearctic fishes. *Molecular Ecology* 7, 431-452.
- Bouton N, Witte F, van Alphen JJ, Seehausen O (1999) Local adaptations in populations of rock-dwelling haplochromines (Pisces: Cichlidae) from southern Lake Victoria. *Proc R Soc Lond B Biol Sci* 266, 366-360.

- Brenner M, Buck B, Cordes S, Dietrich L, Jacob U, Mintenbeck K, Schröder A, Brey T, Knust R, Arntz WE (2001) The role of iceberg scours in niche separation within the Antarctic fish genus *Trematomus*. *Polar Biology* 24 (7), 502-507.
- *Caldera EJ, Bolnick DI (2008) Effects of colonization history and landscape structure on genetic variation within and among threespine stickleback (*Gasterosteus aculeatus*) populations in a single watershed. *Evolutionary Ecology Research* 10, 575-598.
- Carreras-Carbonell J, Macpherson E, Pascual M (2005) Rapid radiation and cryptic speciation in mediterranean triplefin blennies (Pisces: Tripterygiidae) combining multiple genes. *Molecular Phylogenetics and Evolution* 37 (3), 751-761.
- *Carvalho-Costa LF, Hatanka T, Galetti Jr. PM (2008) Evidence of lack of population substructuring in the Brazilian freshwater fish *Prochilodus costatus*. *Genetics and Molecular Biology* 31 (1), 377-380.
- *Chabot CL, Allen LG (2009) Global population structure of the tope (*Galeorhinus galeus*) inferred by mitochondrial control region sequence data. *Molecular Ecology* 18, 545-552.
- *Chauhan T, Lal KK, Mohindra V, Singh R, Punia P, Gopalakrishnan A, Sharma PC, Lakra W (2007) Evaluating genetic differentiation in wild populations of the Indian major carp, *Cirrhinus mrigala* (Hamilton-Buchanan, 1882): Evidence from allozyme and microsatellite markers. *Aquaculture* 269, 135-149.
- Chen L, DeVries AL, Cheng, CHC (1997) Evolution of antifreeze glycoprotein gene from a trypsinogen gene in Antarctic notothenioid fish. *PNAS* 94 (8), 3811-3816.
- *Chen S, Liu T, Li Z, Gao T (2008) Genetic population structuring and demographic history of red spotted grouper (*Epinephelus akaara*) in South and East China Sea. *African Journal of Biotechnology* 7 (20), 3554-3562.
- Cheng CHC, Chen L, Near TJ, Jin Y (2003) Functional antifreeze glycoprotein genes in temperate-water New Zealand nototheniid fish infer an Antarctic evolutionary origin. *Molecular Biology and Evolution* 20 (11), 1897-1908.
- *Chow S, Suzuki N, Brodeur RD, Ueno Y (2009) Little population structuring and recent evolution of the Pacific saury (*Cololabis saira*) as indicated by mitochondrial and nuclear DNA sequence data. *Journal of Experimental Marine Biology and Ecology* 369, 17-21.
- Clark MS, Fraser KPP, Burns G, Peck LS (2008) The HSP70 heat shock response in the Antarctic fish *Harpagifer antarcticus*. *Polar Biology* 31 (2), 171-180.
- Clarke A, Johnston IA (1996) Evolution and adaptive radiation of antarctic fishes. *Trends in Ecology and Evolution* 11 (5), 212-218.
- Cocca E, Ratnayake-Lecamwasam M, Parker SK, Camardella L, Ciaramella M, di Prisco G, Detrich III HW (1995) Genomic remnants of alpha-globin genes in the hemoglobinless antarctic icefishes. *PNAS* 92 (6), 1817-1821.
- Cohen AS, Lezzar KE, Tiercelin JJ, Soreghan M (1997) New paleogeographic and lake-level reconstructions of Lake Tanganyika: implications for tectonic, climatic and biological evolution in a rift lake. *Basin Research* 7, 107-132.
- Coyne JA, Orr HA (2004) *Speciation* Sinauer Associates, Sunderland, Massachusetts.
- *Craig MT, Eble JA, Bowen BW, Robertson DR (2007) High genetic connectivity across the Indian and Pacific Oceans in the reef fish *Myripristis berndti* (Holocentridae). *Marine Ecology Progress Series* 334, 245-254.
- Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK (2000) Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution* 15 (7), 290-295.

- *Curley BG, Gillings MR (2009) Population connectivity in the temperate damselfish *Parma microlepis*: analyses of genetic structure across multiple spatial scales. *Marine Biology* 156 (3), 381-393.
- *Danancher D, Izquierdo JI, Garcia-Vazquez E (2008) Microsatellite analysis of relatedness structure in young of the year of the endangered *Zingel asper* (Percidae) and implications for conservation. *Freshwater Biology* 53 (3), 546-557.
- Dawson MN, Waples RS, Bernardi (2006) Phylogeography. In: *The Ecology of Marine Fishes* (eds. Allan LG, Pondella DJ, Horn MH), pp. 26-54. University of California Press, CA.
- Debes PV, Zachos FE, Hanel R (2008) Mitochondrial phylogeography of the European sprat (*Sprattus sprattus* L., Clupeidae) reveals isolated climatically vulnerable populations in the Mediterranean Sea and range expansion in the northeast Atlantic. *Molecular Ecology* 17, 3873-3888.
- de Graaf M, Dejen E, Osse JWM, Sibbing FA (2008) Adaptive radiation of Lake Tana's (Ethiopia) *Labeobarbus* species flock (Pisces, Cyprinidae). *Marine and Freshwater Research* 59, 391-407.
- Dieckmann U, Doebeli M (1999) On the origin of species by sympatric speciation. *Nature* 400, 354-357.
- *Dillane E, Cross MC, McGinnity P, Coughlan JP, Galvin PT, Wilkins NP, Cross TF (2007) Spatial and temporal patterns in microsatellite DNA variation of wild Atlantic salmon, *Salmo salar*, in Irish rivers. *Fisheries Management and Ecology* 14, 209-219.
- *Dillane E, McGinnity P, Coughlan JP, Cross MC, de Eyto E, Kenchington E, Prodöhl P, Cross TF (2008) Demographics and landscape features determine intrariver population structure in Atlantic salmon (*Salmo salar* L.): the case of the River Moy in Ireland. *Molecular Ecology* 17 (22), 4786-4800.
- Dimitrov D, Arnedo MA, Ribera C (2008) Colonization and diversification of the spider genus *Pholcus* Walckenaer, 1805 (Araneae, Pholcidae) in the Macaronesian archipelagos: evidence for long-term occupancy yet rapid recent speciation. *Molecular Phylogenetics and Evolution* 48, 596-614.
- di Prisco G, Cocca E, Parker SK, Detrich III HW (2002) Tracking the evolutionary loss of hemoglobin expression by the white-blooded Antarctic icefishes. *Gene* 295 (2), 185-191.
- Donaldson TJ (1995). Courtship and spawning of nine species of wrasses (Labridae) from the western Pacific. *Jap J Ichthyol* 42, 311-319.
- *Drew J, Allen GR, Kaufmann L, Barber PH (2008) Endemism and regional color and genetic differences in five putatively cosmopolitan reef fishes. *Conservation Biology* 22 (4), 965-975.
- *Dudgeon CL, Broderick D, Ovenden JR (2009) IUCN classification zones concord with, but underestimate, the population genetic structure of the zebra shark *Stegostoma fasciatum* in the Indo-West Pacific. *Molecular Ecology* 18 (2), 248-261.
- *Duftner N, Sefc KM, Koblmüller S, Nevado B, Verheyen E, Phiri H, Sturmbauer C (2006) Distinct population structure in a phenotypically homogeneous rock-dwelling cichlid fish from Lake Tanganyika. *Mol Ecol* 15, 2381-2395.
- Eastman JT (1993) *Antarctic fish biology: evolution in a unique environment*. Academic Press, San Diego, CA.
- Eastman JT (2005) The nature of the diversity of Antarctic fishes. *Polar Biology* 28, 93-107.

- Eastman JT, Clarke A (1998) A comparison of adaptive radiations of Antarctic fish with those of non-Antarctic fish. In: *Fishes of Antarctica. A biological overview* (eds. di Prisco G, Pisano E, Clarke A), pp. 3-26. Springer, Milan, Italy.
- *Eble JA, Toonen RJ, Bowen BW (2009) Endemism and dispersal: comparative phylogeography of three surgeonfishes across the Hawaiian Archipelago. *Marine Biology* 156 (4), 689-698.
- *Elmer KR, van Houdt JKJ, Meyer A, Volckaert FAM (2008) Population genetic structure of North American burbot (*Lota lota maculosa*) across the Nearctic and at its contact zone with Eurasian burbot (*Lota lota lota*). *Canadian Journal of Fisheries and Aquatic Sciences* 65 (11), 2412-2426.
- Evans CW, Cziko PA, Cheng CHC, DeVries AL (2005) Spawning behaviour and early development in the naked dragonfish *Gymnodraco acuticeps*. *Antarctic Science* 17 (3), 319-327.
- Feulner PG, Kirschbaum F, Mamonekene V, Ketmaier V, Tiedemann R (2007) Adaptive radiation in African weakly electric fish (Teleostei: Mormyridae: Campylomormyrus): a combined molecular and morphological approach. *J Evol Biol* 20, 403-414.
- Floeter SR, Rocha LA, Robertson DR, *et al.* (2008) Atlantic reef fish biogeography and evolution. *Journal of Biogeography* 35, 22-47.
- *Fontaine PM, Dodson JJ, Bernatchez L, Slettan A (1997) A genetic test of metapopulation structure in Atlantic salmon (*Salmo salar*) using microsatellites. *Canadian Journal of Fisheries and Aquatic Sciences* 54 2434-2442.
- *Francisco SM, Cabral H, Vieira MN, Almada VC (2006) Contrasts in genetic structure and historical demography of marine and riverine populations of *Atherina* at similar geographical scales. *Estuarine, Coastal and Shelf Science* 69, 655-661.
- *Froukh T, Kochzius M (2007) Genetic population structure of the endemic fourline wrasse (*Larabicus quadrilineatus*) suggests limited larval dispersal distances in the Red Sea. *Molecular Ecology* 16, 1359-1367.
- *Galarza JA, Carbonell-Carreras J, Macpherson E, Pascual M, Roques S, Turner G, Rico C (2009) The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species. *PNAS* 106 (5), 1473-1478.
- Garant D, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology* 21 (3), 434-443.
- Gavrilets S (2004) *Fitness landscapes and the origin of species*. Princeton University Press, Princeton, New Jersey.
- Gavrilets S, Vose A (2005) Dynamic patterns of adaptive radiation. *Proc Natl Acad Sci U S A* 102, 18040-18045.
- Gavrilets S, Vose A, Barluenga M, Salzburger W, Meyer A (2007) Case studies and mathematical models of ecological speciation. 1. Cichlids in a crater lake. *Mol Ecol* 16, 2893-2909.
- Ghiselin MT (1969) The evolution of hermaphroditism among animals. *Q Rev Biol* 44, 189-208.
- Goodwin NB, Balshine-Earn S, Reynolds JD (1998) Evolutionary transitions in parental care in cichlid fish. *Proc R Soc Lond B Biol Sci* 265, 2265-2272.
- *Goswami M, Thangaraj K, Chaudhary BK, Bjaskar, LVSK, Gopalakrishnan A, Joshi MB, Singh L, Lakra WS (2009) Genetic heterogeneity in the Indian stocks of seahorse

- (*Hippocampus kuda* and *Hippocampus trimaculatus*) inferred from mtDNA cytochrome b gene. *Hydrobiologia* 621, 213-221.
- Grant PR, Grant BR (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296, 707-711.
- Grant PR, Grant BR (2006) Evolution of character displacement in Darwin's finches. *Science* 313, 224-226.
- *Grunwald C, Stabile J, Waldman JR, Gross R, Wirgin I (2002) Population genetics of shortnose sturgeon *Acipenser brevirostrum* based on mitochondrial DNA control region sequences. *Molecular Ecology* 11, 1885-1898.
- *Grunwald C, Maceda L, Waldman JR, Stabile J, Wirgin I (2008) Conservation of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*: delineation of stock structure and distinct population segments. *Conservation Genetics* 9, 1111-1124.
- *Guy TJ, Gresswell RE, Banks MA (2008) Landscape-scale evaluation of genetic structure among barrier-isolated populations of coastal cutthroat trout, *Oncorhynchus clarkii clarkii*. *Canadian Journal of Fisheries and Aquatic Sciences* 65, 1749-1762.
- Hanel R, Westneat MW, Sturmbauer C (2002) Phylogenetic relationships, evolution of broodcare behavior, and geographic speciation in the Wrasse tribe Labrini. *Journal of Molecular Evolution* 55, 776-789.
- *Hatanaka T, Henrique-Silva F, Galetti Jr. PM (2006) Population Substructuring in a Migratory Freshwater Fish *Prochilodus argenteus* (Characiformes, Prochilodontidae) from the São Francisco River. *Genetica* 126, 153-159.
- *Hepburn RI, Sale PF, Dixon B, Heath DD (2009) Genetic structure of juvenile cohorts of bicolor damselfish (*Stegastes partitus*) along the Mesoamerican barrier reef: chaos through time. *Coral Reefs* 28 (1), 277-288.
- Herder F, Nolte AW, Pfaender J, Schwarzer J, Hadiaty RK, Schliewen UK (2006) Adaptive radiation and hybridization in Wallace's Dreamponds: evidence from sailfin silversides in the Malili Lakes of Sulawesi. *Proc Biol Sci* 273, 2209-2217.
- Hey J, Nielsen R (2007) Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. *PNAS* 104 (8), 2785-2790.
- *Hickey AJR, Lavery SD, Hannan DA, Baker CS, Clements KD (2009) New Zealand triplefin fishes (family Tripterygiidae): contrasting population structure and mtDNA diversity within a marine species flock. *Molecular Ecology* 18, 680-696.
- Higashi M, Takimoto G, Yamamura N (1999) Sympatric speciation by sexual selection. *Nature* 402, 523-526.
- Hofmann GE, Buckley BA, Airaksinen S, Keen JE, Somero GN (2000) Heat-shock protein expression is absent in the antarctic fish *Trematomus bernacchii* (family Nototheniidae). *Journal of Experimental Biology* 203 (15), 2331-2339.
- *Horne JB, van Herwerden L, Choat JH, Robertson DR (2008) High population connectivity across the Indo-Pacific: Congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution* 49 (2), 629-638.
- *Hrbek T, Farias IP, Crossa M, Sampaio I, Porto JIR, Meyer A (2005) Population genetic analysis of *Arapaima gigas*, one of the largest freshwater fishes of the Amazon basin: implications for its conservation. *Animal Conservation* 8, 297-308.
- Hsü KJ, Montadert L, Bernoulli D, Cita MB, Erickson A, Garrison RE, Kidd RB, Mèlières F, Müller C, Wright R (1977) History of the Mediterranean salinity crisis. *Nature* 267, 399-403.

- Hsü KJ, Ryan WBF, Cita MB (1973) Late Miocene desiccation of the Mediterranean. *Nature* 242, 240-244.
- *Hubert N, Duponchelle F, Nuñez J, Rivera R, Bonhomme F, Renno JF (2007) Isolation by distance and Pleistocene expansion of the lowland populations of the white piranha *Serrasalmus rhombeus*. *Molecular Ecology* 16, 2488-2503.
- Hulsey (2006) Function of a key morphological innovation: fusion of the cichlid pharyngeal jaw. *Proc Biol Sci* 263, 669-675.
- Janko K, Lecointre G, DeVries AL, Couloux A, Cruaud C, Marshall C (2007) Did glacial advances during the Pleistocene influence differently the demographic histories of benthic and pelagic Antarctic shelf fishes? - Inferences from intraspecific mitochondrial and nuclear DNA sequence diversity. *BMC Evolutionary Biology* 7, 220.
- Johnson TC, Scholz CA, Talbot MR, Kelts K, Ricketts RD, Ngobi G, Beuning K, Ssemmanda II, McGill JW (1996) Late Pleistocene Desiccation of Lake Victoria and Rapid Evolution of Cichlid Fishes. *Science* 273, 1091-1093.
- *Jones CD, Anderson ME, Balushkin AV, Duhamel G, Eakin RR, Eastman JT, Kuhn KL, Lecointre G, Near TJ, North AW, Stein DL, Vacchi M, Detrich III HW (2008) Diversity, relative abundance, new locality records and population structure of Antarctic demersal fishes from the northern Scotia Arc islands and Bouvetøya. *Polar Biology* 31, 1481-1497.
- Juan C, Ibrahim KM, Oromí P, Hewitt GM (1998) The phylogeography of the darkling beetle, *Hegeter politus*, in the eastern Canary Islands. *Proceedings of the Royal Society of London B: Biological Sciences* 265 (1391), 135-140.
- Kazancioglu E, Near TJ, Hanel R, Wainwright PC (2009) Influence of feeding functional morphology and sexual selection on diversification rate of parrotfishes (Scaridae). Submitted to *Proceedings of the Royal Society B*.
- Kellermann AK (1991) Egg and larval drift of the Antarctic fish *Notothenia coriiceps*. *Cybius* 15 (3), 199-210.
- *Kitanishi S, Yamamoto T, Higashi S (2009) Microsatellite variation reveals fine-scale genetic structure of masu salmon, *Oncorhynchus masou*, within the Atsuta River. *Ecology of Freshwater Fish* 18, 65-71.
- Klingenberg CP, Ekau W (1996) A combined morphometric and phylogenetic analysis of an ecomorphological trend: pelagization in Antarctic fishes (Perciformes: Nototheniidae). *Biological Journal of the Linnean Society* 59, 143-177.
- Kocher TD (2004) Adaptive evolution and explosive speciation: the cichlid fish model. *Nature Reviews Genetics* 5, 288-298.
- Kock KH (2005) Antarctic icefishes (Channichthyidae): a unique family of fishes. A review, part I. *Polar Biology* 28 (11), 862-895.
- Kock KH, Kellermann AK (1991) Reproduction in Antarctic notothenioid fish. *Antarctic Science* 3 (2), 125-150.
- Kock KH, Pshenichnov LK, DeVries AL (2006) Evidence for egg brooding and parental care in icefish and other notothenioids in the Southern Ocean. *Antarctic Science* 18 (2), 223-227.
- Kondrashov AS, Kondrashov FA (1999) Interactions among quantitative traits in the course of sympatric speciation. *Nature* 400, 351-354.
- Kornfield I, Carpenter KE (1984) Cyprinids of Lake Lanao, Philippines: Taxonomic validity, evolutionary rates and speciation scenarios. In: *Evolution of Fish Species Flocks* (eds. Echelle AA, Kornfield I), pp. 69-84. University of Maine at Orono Press, Orono, Maine.

- Kornfield I, Smith PF (2000) African Cichlid Fishes: Model systems for evolutionary biology. *Annu. Rev. Ecol. Syst.* 31, 163-196.
- *Kuhn KL, Gaffney PM (2006) Preliminary assessment of population structure in the mackerel icefish (*Champscephalus gunnari*). *Polar Biology* 29, 927-935.
- La Mesa M, Ashford J (2008) Age and early life history of juvenile scotia sea icefish, *Chaenocephalus aceratus*, from Elephant and the South Shetland Islands. *Polar Biology* 31 (2), 221-228.
- Leis JM (2006) Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology* 51, 57-141.
- Lessios HA (1998) The first stage of speciation as seen in organisms separated by the Isthmus of Panama. In: *Endless Forms: Species and Speciation* (eds. Howard DH, Berlocher SH), pp. 186-201. Oxford University Press, Oxford, UK.
- Liem KF (1973) Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* 22, 425-441.
- *Lin J, Quinn TP, Hilborn R, Hauser L (2008a) Fine-scale differentiation between sockeye salmon ecotypes and the effect of phenotype on straying. *Heredity* 101 (4), 341-350.
- *Lin J, Zigel E, Quinn TP, Hauser L (2008b) Contrasting patterns of morphological and neutral genetic divergence among geographically proximate populations of sockeye salmon *Oncorhynchus nerka* in Lake Aleknagik, Alaska. *Journal of Fish Biology* 73 (8), 1993-2004.
- Loeb VJ, Kellermann AK, Koubbi P, North AW, White MG (1993) Antarctic larval fish assemblages: a review. *Bulletin of Marine Science* 53 (2), 416-449.
- Lourie SA, Vincent ACJ (2004) A marine fish follows Wallace's Line: the phylogeography of the three-spot seahorse (*Hippocampus trimaculatus*, Syngnathidae, Teleostei) in Southeast Asia. *Journal of Biogeography* 31, 1975-1985.
- Losos JB, Jackmann TR, Larson A, De Queiroz K, Rodrigues-Schettino L (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279, 2115-2118.
- Luterbacher HP, Ali JR, Brinkhuis H, Gradstein FM, Hooker JJ, Monechi S, Ogg JG, Powell J, Röhl U, Sanfilippo A, Schmitz B (2004) The Paleogene period. In: *A geologic time scale* (ed. Gradstein F, Ogg J, Smith A), pp. 384-408. Cambridge University Press, Cambridge.
- Mabuchi K, Miya M, Azuma Y, Nishida M (2007) Independent evolution of the specialized pharyngeal jaw apparatus in cichlid and labrid fishes. *BMC Evol Biol* 7, 10.
- *Markert JA, Arnegard ME, Danley PD, Kocher TD (1999) Biogeography and population genetics of the Lake Malawi cichlid *Melanochromis auratus*: habitat transience, philopatry and speciation. *Molecular Ecology* 8, 1013-1026.
- *Matschiner M, Hanel R, Salzburger W (2009) Gene flow by larval dispersal in the Antarctic notothenioid fish *Gobionotothen gibberifrons*. *Molecular Ecology*, in press.
- Mayr E (1942) *Systematics and the Origin of Species* Columbia University Press, New York.
- Mayr E (1963) *Animal Species and Evolution* Harvard University Press, Cambridge.
- McCune AR (1997) How fast is speciation? Molecular, geological and phylogenetic evidence from adaptive radiations of fishes. In: *Molecular evolution and adaptive radiation* (eds. Givnish TJ, Sytsma KJ), pp. 585-610. Cambridge University Press, Cambridge, UK.

- *Miller-Sims VC, Gerlach G, Kingsford MJ, Atema J (2008) Dispersal in the spiny damselfish, *Acanthochromis polyacanthus*, a coral reef fish species without a larval pelagic stage. *Molecular Ecology* 17 (23), 5036-5048.
- Moritz C (1994) Defining 'Evolutionary Significant Units' for conservation. *Trends in Ecology and Evolution* 9 (10), 373-375.
- Muss A, Robertson DR, Stepien CA, Wirtz P, Bowen BW (2001) Phylogeography of *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution* 55 (3), 561-572.
- Mwanja WW, Armoudlian AS, Wandera SB, Kaufmann L, Wu L, Booton GC, Fuerst PA (2001) The bounty of minor lakes: the role of small satellite water bodies in evolution and conservation of fishes in the Lake Victoria Region, East Africa. *Hydrobiologia* 458, 55-62.
- Near TJ (2004) Estimating divergence times of notothenioid fishes using a fossil-calibrated molecular clock. *Antarctic Science* 16, 37-44.
- Near TJ, Cheng CHC (2008) Phylogenetics of notothenioid fishes (Teleostei: Acanthomorpha): inferences from mitochondrial and nuclear gene sequences. *Mol Phylogenet Evol* 47, 832-840.
- Near TJ, Parker SK, Detrich III HW (2006) A genomic fossil reveals key steps in hemoglobin loss by the antarctic icefishes. *Molecular Biology and Evolution* 23 (11), 2008-2016.
- *Neethling M, Matthee CA, Bowie RCK, von der Heyden S (2008) Evidence for panmixia despite barriers to gene flow in the southern African endemic, *Caffrogobius caffer* (Teleostei: Gobiidae). *BMC Evolutionary Biology* 8, 325.
- Nelson JS (2006) *Fishes of the World*.
- Nepokroeff M, Sytsma KJ, Wagner WL, Zimmer EA (2003) Reconstructing ancestral patterns of colonization and dispersal in the Hawaiian understory tree genus *Psychotria* (Rubiaceae): A comparison of parsimony and likelihood approaches. *Systematic Biology* 52 (6), 820-838.
- *Osinov AG, Gordeeva NV (2008) Variability of the microsatellite DNA and genetic differentiation of the populations of residual form of Dolly varden trout *Salvelinus malma krascheninnikovi* of Sakhalin. *Journal of Ichthyology* 48 (9), 691-706.
- Ostbye K, Bernatchez L, Naesje TF, Himberg KJ, Hindar K (2005) Evolutionary history of the European whitefish *Coregonus lavaretus* (L.) species complex as inferred from mtDNA phylogeography and gill-raker numbers. *Mol Ecol* 14, 4371-4387.
- *Pálsson S, Kállman T, Paulsen J, Árnason E (2009) An assessment of mitochondrial variation in Arctic gadoids. *Polar Biology* 32 (3), 471-479.
- Palumbi SR (1994) Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* 25, 547-572.
- Papetti C, Liò P, Rüber L, Patarnello T, Zardoya R (2007a) Antarctic fish mitochondrial genomes lack ND6 gene. *Journal of Molecular Evolution* 65 (5), 519-528.
- *Papetti C, Susana E, La Mesa M, Kock KH, Patarnello T, Zane L (2007b) Microsatellite analysis reveals genetic differentiation between year-classes in the icefish *Chaenocephalus aceratus* at South Shetlands and Elephant Island. *Polar Biology* 30 (12), 1605-1613.
- Parenti LR (1984) Biogeography of the Andean killifish genus *Orestias* with comments on the species flock concept. In: *Evolution of Fish Species Flocks* (eds. Echelle AA, Kornfield I), pp. 85-92. University of Maine at Orono Press, Orono, Maine.

- Parenti P, Randall JE (2000) An annotated checklist of the species of the labroid fish families Labridae and Scaridae. *Ichthyol. Bull. (J.L.B. Smith Inst.)* 68, 1–97.
- *Patarnello T, Marcato S, Zane L, Varotto V, Bargelloni L (2003) Phylogeography of the Chionodraco genus (Perciformes, Channichthyidae) in the Southern Ocean. *Molecular Phylogenetics and Evolution* 28, 420-429.
- Patarnello T, Volckaert FJ, Castilho R (2007) Pillars of Hercules: is the Atlantic-Mediterranean transition a phylogeographical break? *Molecular Ecology* 16, 4426-4444.
- Patterson C (1993) Vertebrates, Osteichthyes: Teleostei. In: *The fossil record 2* (ed. Benton MJ), pp. 621-657. Chapman & Hall, London, UK.
- *Pereyra R, Taylor MI, Turner GF, Rico C (2004) Variation in habitat preference and population structure among three species of the Lake Malawi cichlid genus *Protomelas*. *Mol Ecol* 13, 2691-2697.
- Policansky D (1982) Sex change in animals and plants. *Ann Rev Ecol Syst* 13, 471-495.
- *Prodocimo V, Tschá MK, Pie MR, Oliveira-Neto JF, Ostrensky A, Boeger WA (2008) Lack of genetic differentiation in the fat snook *Centropomus parallelus* (Teleostei: Centropomidae) along the Brazilian coast. *Journal of Fish Biology* 73 (8), 2075-2082.
- Puebla O, Bermingham E, Guichard F (2008) Population genetic analyses of *Hypoplectrus* coral reef fishes provide evidence that local processes are operating during the early stages of marine adaptive radiations. *Mol Ecol* 17, 1405-1415.
- Puebla O, Bermingham E, Guichard F, Whiteman E (2007) Colour pattern as a single trait driving speciation in *Hypoplectrus* coral reef fishes? *Proc Biol Sci* 274, 1265-1271.
- *Ramon ML, Nelson PA, Martini E, Walsh WJ, Bernardi G (2008) Phylogeography, historical demography, and the role of post-settlement ecology in two Hawaiian damselfish species. *Marine Biology* 153, 1207-1217.
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanog (Miami)* 5, 655–847.
- Reinboth R (1970) Intersexuality in fishes. *Mem Soc Endocr* 18, 515-543.
- Rice WR (1989) Analysing tables of statistical tests. *Evolution* 43, 223-225.
- Rico C, Bouteillon P, van Oppen MJ, Knight ME, Hewitt GM, Turner GF (2003) No evidence for parallel sympatric speciation in cichlid species of the genus *Pseudotropheus* from north-western Lake Malawi. *J Evol Biol* 16, 37-46.
- *Rico C, Turner GF (2002) Extreme microallopatric divergence in a cichlid species from Lake Malawi. *Mol Ecol* 11, 1585-1590.
- *Rivera MAJ, Kelley CD, Roderick GK (2004) Subtle population genetic structure in the Hawaiian grouper, *Epinephelus quernus* (Serranidae) as revealed by mitochondrial DNA analyses. *Biological Journal of the Linnean Society* 81, 449-468.
- *Rocha LA, Bass AL, Robertson DR, Bowen BW (2002) Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Molecular Ecology* 11, 243-252.
- Rocha LA, Bowen BW (2008) Speciation in coral-reef fishes. *Journal of Fish Biology* 72, 1101-1121.
- Rocha LA, Craig MT, Bowen BW (2007) Phylogeography and the conservation of coral reef fishes. *Coral Reefs* 26 (3), 501-512.
- Rocha LA, Rocha CR, Robertson DR, Bowen BW (2008) Comparative phylogeography of Atlantic reef fishes indicates both origin and accumulation of diversity in the Caribbean. *BMC Evol Biol* 8, 157.

- *Rogers AD, Morley S, Fitzcharles E, Jarvis K, Belchier M (2006) Genetic structure of Patagonian toothfish (*Dissostichus eleginoides*) populations on the Patagonian Shelf and Atlantic and western Indian Ocean Sectors of the Southern Ocean. *Marine Biology* 149, 915-924.
- Rögl F (1999) Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene palaeogeography (short overview). *Geologica Carpathica* 50 (4), 339-349.
- Rossiter A (1995) The cichlid fish assemblages of Lake Tanganyika: ecology, behavior and evolution of its species flocks. *Advances in Ecological Research* 26, 157-252.
- Roy D, Docker MF, Haffner GD, Heath DD (2007a) Body shape vs. colour associated initial divergence in the *Telmatherina* radiation in Lake Matano, Sulawesi, Indonesia. *J Evol Biol* 20, 1126-1137.
- Roy D, Paterson G, Hamilton PB, Heath DD, Haffner GD (2007b) Resource-based adaptive divergence in the freshwater fish *Telmatherina* from Lake Matano, Indonesia. *Mol Ecol* 16, 35-48.
- Rüber L, Van Tassell JL, Zardoya R (2003) Rapid speciation and ecological divergence in the American seven-spined gobies (Gobiidae, Gobiomatini) inferred from a molecular phylogeny. *Evolution* 57, 1584-1598.
- Rüber L, Zardoya R (2005) Rapid cladogenesis in marine fishes revisited. *Evolution Int J Org Evolution* 59, 1119-1127.
- Ruud JT (1954) Vertebrates without erythrocytes and blood pigment. *Nature* 173 (4410), 848-850.
- Ryder OA (1986) Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution*. 1, 9-10.
- *Saito T, Washio S, Dairiki K, Shimojo M, Itoi S, Sugita H (2008) High gene flow in *Girella punctata* (Perciformes, Kyphosidae) among the Japanese Islands inferred from partial sequence of the control region in mitochondrial DNA. *Journal of Fish Biology* 73 (8), 1937-1945.
- Salzburger W (2008) To be or not to be a hamlet pair in sympatry. *Mol Ecol* 17, 1397-1399.
- Salzburger W (2009) The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes. *Mol Ecol* 18, 169-185.
- Salzburger W, Brandstätter A, Gilles A, Parson W, Hempel M, Sturmbauer C, Meyer A (2003) Phylogeography of the vairone (*Leuciscus souffia*, Risso 1826) in Central Europe. *Molecular Ecology* 12 (9), 2371-2386.
- Salzburger W, Mack T, Verheyen E, Meyer A (2005) Out of Tanganyika: Genesis, explosive speciation, key-innovations and phylogeography of the haplochromine cichlid fishes. *BMC Evolutionary Biology* 5, 17.
- Salzburger W, Meyer A (2004) The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. *Naturwissenschaften* 91, 277-290.
- Sanchez S, Dettai A, Bonillo C, Ozouf-Costaz C, Detrich III HW, Lecointre G (2007) Molecular and morphological phylogenies of the Antarctic teleostean family Nototheniidae, with emphasis on the Trematominae. *Polar Biology* 30, 155-166.
- *Santos MCF, Ruffino ML, Farias IP (2007) High levels of genetic variability and panmixia of the tambaqui *Colossoma macropomum* (Cuvier, 1816) in the main channel of the Amazon River. *Journal of Fish Biology* 71, 33-44.

- Savolainen V, Anstett MC, Lexer C, *et al.* (2006) Sympatric speciation in palms on an oceanic island. *Nature* 441, 210-213.
- Schliewen UK, Tautz D, Paabo S (1994) Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368, 629-632.
- Schluter D (2000) *The Ecology of Adaptive Radiation* Oxford University Press, New York.
- Schluter D, McPhail JD (1992) Ecological character displacement and speciation in sticklebacks. *American Naturalist* 140, 85-108.
- *Schultz JK, Feldheim KA, Gruber SH, Ashley MV, McGovern TM, Bowen BW (2008) Global phylogeography and seascape genetics of the lemon sharks (genus *Negaprion*). *Molecular Ecology* 17 (24), 5336-5348.
- Seehausen O (2002) Patterns in fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14,600 year history for its cichlid species flock. *Proc R Soc Lond B Biol Sci* 269, 491-470.
- Seehausen O (2006) African cichlid fish: a model system in adaptive radiation research. *Proc Biol Sci* 273, 1987-1998.
- *Sefc KM, Baric S, Salzburger W, Sturmbauer C (2007) Species-specific population structure in rock-specialized sympatric cichlid species in Lake Tanganyika, East Africa. *J Mol Evol* 64, 33-49.
- Sequeira AS, Lanteri AA, Albelo LR, Bhattacharya S, Sijapati M (2008) Colonization history, ecological shifts and diversification in the evolution of endemic Galápagos weevils. *Molecular Ecology* 17 (4), 1089-1107.
- Shaw KL (1996) Sequential Radiations and Patterns of Speciation in the Hawaiian Cricket Genus *Laupala* Inferred from DNA Sequences. *Evolution* 50 (1), 237-255.
- *Shaw PW, Arkhipkin A, Al-Khairulla A (2004) Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Molecular Ecology* 13, 3293-3303.
- *Shaw PW, Turner GF, Idid MR, Robinson RL, Carvalho GR (2000) Genetic population structure indicates sympatric speciation of Lake Malawi pelagic cichlids. *Proc R Soc Lond B Biol Sci* 267, 2273-2280.
- *Silva-Oliveira GC, do Rêgo PS, Schneider H, Sampaio I, Vallinoto M (2008) Genetic characterisation of populations of the critically endangered Goliath grouper (*Epinephelus itajara*, Serranidae) from the Northern Brazilian coast through analyses of mtDNA. *Genetics and Molecular Biology* 31 (4), 988-994.
- Smith CL (1967) Contribution to a theory of hermaphroditism. *Journal of Theoretical Biology* 17, 76-90.
- Smith CL (1975) The evolution of hermaphroditism in fishes. In: *Intersexuality in the Animal Kingdom* (ed. Reinboth R), pp. 295-310. Springer Verlag, New York.
- *Smith PJ, Gaffney PM (2005) Low genetic diversity in the Antarctic toothfish (*Dissostichus mawsoni*) observed with mitochondrial and intron DNA markers. *CCAMLR Science* 12, 43-51.
- Stager JC, Johnson TC (2008) The late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. *Hydrobiologia* 596, 5-16.
- Stearns SC (1976) Life-history tactics: a review of the ideas. *Q Rev Biol* 51, 3-45.
- *Stepien CA, Murphy DJ, Strange RM (2007) Broad- to fine-scale population genetic patterning in the smallmouth bass *Micropterus dolomieu* across the Laurentian Great

- Lakes and beyond: an interplay of behaviour and geography. *Molecular Ecology* 16, 1605-1624.
- *Streelman JT, Albertson RC, Kocher TD (2007) Variation in body size and trophic morphology within and among genetically differentiated populations of the cichlid fish, *Metriaclima zebra*, from Lake Malawi. *Freshwater Biology* 52 (3), 525-538.
- Streelman JT, Alfaro M, Westneat MW, Bellwood DR, Karl SA (2002) Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. *Evolution* 56, 961-971.
- Sturmbauer C (1998) Explosive speciation in cichlid fishes of the African Great Lakes: a dynamic model of adaptive radiation. *Journal of Fish Biology* 53 (Supplement A), 18-36.
- Sturmbauer C, Baric S, Salzburger W, Rüber L, Verheyen E (2001) Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. *Mol Biol Evol* 18, 144-154.
- Sturmbauer C, Hainz U, Baric S, Verheyen E, Salzburger W (2003) Evolution of the tribe Tropheini from Lake Tanganyika: synchronized explosive speciation producing multiple evolutionary parallelism. *Hydrobiologia* 500, 51-64.
- Taberlet P, Fumagalli L, Wust-Saucy A, Cosson J (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* 7, 453-464.
- *Taylor MI, Verheyen E (2001) Microsatellite data reveals weak population substructuring in *Copadichromis* sp. 'virginalis kajose', a demersal cichlid from Lake Malawi, Africa. *Journal of Fish Biology* 59, 593-604.
- Taylor MS, Hellberg ME (2005) Marine radiations at small geographic scales: speciation in neotropical reef gobies (*Elacatinus*). *Evolution* 59, 374-385.
- *Teterina VI, Sukhanova LV, Bogdanov BE, Anoshko PN, Kirilchik SV (2005) Genetic polymorphism of a pelagic fish species, little Baikal oilfish *Comephorus dybowski*, deduced from analysis of microsatellite loci. *Animal Genetics* 41 (7), 750-754.
- Thatje S, Hillenbrand CD, Larter R (2005) On the origin of Antarctic marine benthic community structure. *Trends in Ecology and Evolution* 20 (10), 534-540.
- *Tinti F, di Nunno C, Guarniero I, Talenti M, Tommasini S, Fabbri E, Picinetti C (2002) Mitochondrial DNA sequence variation suggests the lack of genetic heterogeneity in the Adriatic and Ionian stocks of *Sardina pilchardus*. *Marine Biotechnology* 4, 163-172.
- *van Oppen MJ, Turner GF, Rico C, Deutsch JC, Ibrahim KM, Robinson RL, Hewitt GM (1997) Unusually fine-scale genetic structuring found in rapidly speciating Malawi cichlid fishes. *Proc R Soc Lond B Biol Sci* 264, 1803-1812.
- *Vasconcellos AV, Vianna P, Paiva PC, Schama R, Solé-Cava A (2008) Genetic and morphometric differences between yellowtail snapper (*Ocyurus chrysurus*, Lutjanidae) populations of the tropical West Atlantic. *Genetics and Molecular Biology* 31, 308-316.
- Verheyen E, Salzburger W, Snoeks J, Meyer A (2003) Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* 300, 325-329.
- Veron JEN (1995) *Corals in space and time: biogeography and evolution of the Scleractinia*. Comstock/Cornell, Ithaca, NY.
- *Vonlanthen P, Excoffier L, Bittner D, Persat H, Neuenschwander S, Largiadèr CR (2007) Genetic analysis of potential postglacial watershed crossings in Central Europe by the bullhead (*Cottus gobio* L.). *Molecular Ecology* 16, 4572-4584.

- Vonlanthen P, Roy D, Hudson AG, Largiadere CR, Bittner D, Seehausen O (2009) Divergence along a steep ecological gradient in lake whitefish (*Coregonus* sp.). *J Evol Biol* 22, 498-514.
- Wainwright PC, Bellwood DR, Westneat MW, Grubich JR, Hoey AS (2004) A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biological Journal of the Linnean Society* 82, 1-25.
- *Walter RP, Haffner GD, Heath DD (2009) Dispersal and population genetic structure of *Telmatherina antoniae*, an endemic freshwater Sailfin silverside from Sulawesi, Indonesia. *Journal of Evolutionary Biology* 22 (2), 314-323.
- Westneat MW (1997) Phylogenetic relationships of labrid fishes: an analysis of morphological characters. *Am Zool* 37, 198A.
- Westneat MW (1999) The living marine resources of the Western Central Pacific: FAO species identification sheets for fishery purposes. Family Labridae. *Food and Agriculture Organization of the United Nations* 6, 3381-3467.
- Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Molecular Phylogenetics and Evolution* 36, 370-390.
- White MG (1998) Development, dispersal and recruitment - a paradox for survival among Antarctic fish. In: *Fishes of Antarctica. A biological overview* (eds. di Prisco G, Pisano E, Clarke A). Springer-Verlag, Milano, Italy.
- Williams GC (1966) *Adaptation and natural selection. A critique of some current evolutionary thought*. Princeton University Press, Princeton.
- Wu C-I (2001) The genic view of the process of speciation. *J Evol Biol* 14, 851-865.
- *Wu GCC, Chiang HC, Chen KS (2009) Population structure of albacore (*Thunnus alalunga*) in the Northwestern Pacific Ocean inferred from mitochondrial DNA. *Fisheries Research* 95, 125-131.
- *Xiao Y, Takahashi M, Yanagimoto T, Zhang Y, Gao T, Yabe M, Sakurai Y (2008) Genetic variation and population structure of willow flounder *Tanakius kitaharai* collected from Aomori, Ibaraki and Niigata in Northern Japan. *African Journal of Biotechnology* 7 (21), 3836-3844.
- *Zane L, Bargelloni L, Bortolotto E, Papetti C, Simonato M, Varotto V, Patarnello T (2006) Demographic history and population structure of the Antarctic silverfish *Pleuragramma antarcticum*. *Molecular Evolution*, 15 (14), 4499-4511.