

## INVITED REVIEWS AND SYNTHESSES

**Speciation in fishes**

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The field of speciation has seen much renewed interest in the past few years, with theoretical and empirical advances that have moved it from a descriptive field to a predictive and testable one. The goal of this review is to provide a general background on research on speciation as it pertains to fishes. Three major components to the question are first discussed: the spatial, ecological and sexual factors that influence speciation mechanisms. We then move to the latest developments in the field of speciation genomics. Affordable and rapidly available, massively parallel sequencing data allow speciation studies to converge into a single comprehensive line of investigation, where the focus has shifted to the search for speciation genes and genomic islands of speciation. We argue that fish present a very diverse array of scenarios, making them an ideal model to study speciation processes.

*Keywords:* ecological genetics, evolutionary theory, fish, speciation

*Received 14 May 2013; revision received 8 August 2013; accepted 14 August 2013*

In the past two decades the field of speciation has seen a renewed interest with major theoretical and empirical advances (Rice & Hostert 1993; Howard & Berlocher 1998), accompanied by the publication of seminal books that placed the field within a strong theoretical framework (Coyne & Orr 2004; Dieckman *et al.* 2004; Gravelles 2004; Price 2007; Nosil 2012). Molecular approaches applied to aquatic organisms have traditionally lagged behind their terrestrial counterparts, and this also applies to the field of speciation. In a few cases, however, fishes have been at the forefront of speciation studies. Examples of parallel divergence of sympatric sticklebacks and runaway antagonistic sexual selection in cichlids, which will be discussed later, come to mind (Rundle & Schluter 2004; Parnell & Streelman 2013). The goal of this study is to review the state of knowledge of speciation in fishes and synthesize its idiosyncrasies and breakthroughs.

As there are numerous definitions, a treatment on species concepts goes beyond the scope of this review (De Queiroz 1998; Richards 2010; Hausdorf 2011; Carstens *et al.* 2013). Early species concepts mostly

influenced by Mayr's biological species concept (BSC) assumed some level of reproductive isolation (Mayr 1942). This concept, however, is clearly insufficient even for some simple cases, such as asexual and unisexual species, but also cannot accommodate for the fundamental and growing evidence of speciation in the absence of breeding barriers (Coyne & Orr 2004). Hausdorf (2013) argues that defining species as units that reach fitness maxima, and where any exchange would lower their fitness, encompass most situations and may tend towards a universal species concept. Importantly, many studies that will be mentioned in this review are more concerned by the speciation mechanisms rather than the end product of the species. So for all practical purposes, we will be using Hausdorf's species concept (Hausdorf 2011) as it will suffice for our discussion.

Understanding how divergence emerges, which is the study of speciation, is a question that has been approached in fishes using three different angles. One approach considers the spatial and geographical component of speciation, another tack has focused on the ecological component of speciation, and a third has mostly considered the sexual part of the equation. These three approaches do intersect, at times rather significantly, but for clarity's sake, we will distinguish them here. All three aspects of speciation are rooted in traditional studies and are entering the realm of genomics, making

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a review of the material timely. Thus, this study, which is constrained by its size, will limit itself by first providing a general background on fish, their taxonomy and genomics, then will describe the history of the three approaches to the study of speciation and their latest developments, and will conclude by trying to bring them together for a comprehensive view of the question.

#### *What are fishes?—general background*

Fish are a paraphyletic group of vertebrates that have evolved for the past 500 My and comprise approximately 30 000 species (Nelson 2006). Similarly to other groups of organisms, fish species diversification is not particularly related to the age of the group (Rabosky *et al.* 2012). Fish include the agnathans (jawless fishes: hagfish and lampreys, with about 70 species) and the gnathostomes, which are jawed vertebrates that comprise the chondrichthyans (cartilaginous fishes: chimaeras, sharks and rays, with about 1000 species), the actinopterygians (ray-finned fishes, with more than 25 000 species) and the sarcopterygians (lobe-finned fishes: lungfishes and coelacanths, 11 species) that are closely related to tetrapods (Nelson 2006). While 2.8% of the earth's water is fresh and 2.7909% is not usable by fish, approximately 35% of fish species are found in freshwater. Therefore, freshwater habitats are about 10 000 times more speciose than marine ones, although this may be more a reflection of an ancient marine extinction rather than an actual mechanistic cause (Vega & Wiens 2012). The centre of marine fish diversity is the coral triangle, an area bound by the Philippines, Indonesia and Papua New Guinea, where the highest diversity of marine reef fishes is found, with approximately 2500–4000 species, mostly belonging to the order Perciformes (Carpenter & Springer 2005; Allen 2008; Allen & Erdmann 2012). The centre of freshwater fish diversity is the Amazon Basin, with approximately 2600 species, mostly belonging to the superorder Ostariophysi (catfish, piranhas; Albert & Reis 2011; Chen *et al.* 2013). Most fishes are oviparous, and females produce eggs, which are either released in the water (broadcast spawners) or laid on a surface (benthic spawners; Helfman *et al.* 2009). In marine fishes, eggs (for broadcast spawners) or larvae (for benthic spawners) move with currents and disperse during a pelagic phase, which typically lasts from a few days to several weeks (pelagic larval duration or PLD; Leis 1991), as opposed to freshwater systems where most species do not have pelagic eggs (Kunz-Ramsey 2008). Parental care, generally in the form of male guarding, is common in fishes (Gross & Sargent 1985). A few species of marine fishes lack a pelagic larval stage (apelagic fishes), by either brooding

their offspring (surfperches, Embiotocidae), mouthbrooding (Banggai cardinalfish, *Pterapogon kauderni*) or guarding their babies (some damselfishes, *Acanthochromis polyacanthus*, *Altrichthys azurelineatus*, *A. curatus*; Bernardi 2011). The genetic effects of such different life histories also have a strong influence on the population structure of these species (Doherty *et al.* 1995). Fishes mature at very small sizes (<1 cm, *Paedocypris progenetica*, *Trimmatom nanus* and *Schindleria brevipinguis*) or very large ones (whale shark, *Rhincodon typus*, about 10 m), and their lifespan varies between <1 year (annual killifishes, e.g. *Cynolebias*, *Notobranchius*) to more than 150 years (e.g. rockfishes of the genus *Sebastes*). Taken together, these characteristics result in variations in mutation rates and are to be considered when estimating divergence and coalescence times.

#### *Fish genomics*

Vertebrate genomes have undergone an early duplication (1R) that was followed by a secondary duplication (2R; Ohno 1970). In ray-finned fishes, a third round of duplication, termed 'fish-specific genome duplication' (FSGD, 3R), occurred (Ohno 1970; Taylor *et al.* 2003; Meyer & Van de Peer 2005; Steinke *et al.* 2006; Kuraku & Meyer 2010). Further duplication events may have happened in additional lineages, most notably in salmonids where a recent (50–100 Mya) duplication is well documented (Allendorf & Thorgaard 1984; Koop & Davidson 2008). In general, fish DNA base composition is relatively homogeneous along the genome, resulting in symmetrical peaks in denaturation curves and caesium chloride (CsCl) ultracentrifugation gradients (Bernardi & Bernardi 1990; Bucciarelli *et al.* 2002), which also translates in weak banding patterns in fish chromosomes (Medrano *et al.* 1988). The size range of fish genomes, a value known for more than 40 years (Hinegardner & Rosen 1972), varies widely from the smallest size in some puffers (390 Mb, about one-eighth of the human genome) to more than 300 times that size in *Protopterus aethiopicus* (marbled lungfish, 130 000 Mb, about 40 times the human genome; Metcalfe *et al.* 2012). The difference in size is reflected by a large difference in repeated sequences and transposable elements (Pizon *et al.* 1984), which in turn prompted the early sequencing of the genome of puffers *Takifugu rubripes* and *Tetraodon fluviatilis* (Brenner *et al.* 1993; Jaillon *et al.* 2004). A number of additional fish genomes were sequenced in succession, including zebrafish, medaka, stickleback and tilapia (Colosimo *et al.* 2005; Kasahara *et al.* 2007; Guyon *et al.* 2012; Howe *et al.* 2013). Many fish genomes are currently being sequenced, with an additional several hundreds being targeted in the near future (Bernardi *et al.* 2012a,b). Besides the sequencing of entire

genomes, scanning approaches that give a comprehensive picture of the salient characteristics of a genome, such as restriction site-associated DNA (RAD) sequencing, have been applied to fishes, in particular to sticklebacks, salmonids and whitefish (Hohenlohe *et al.* 2010a; Gagnaire *et al.* 2012a,b; Limborg *et al.* 2012).

### Spatial component

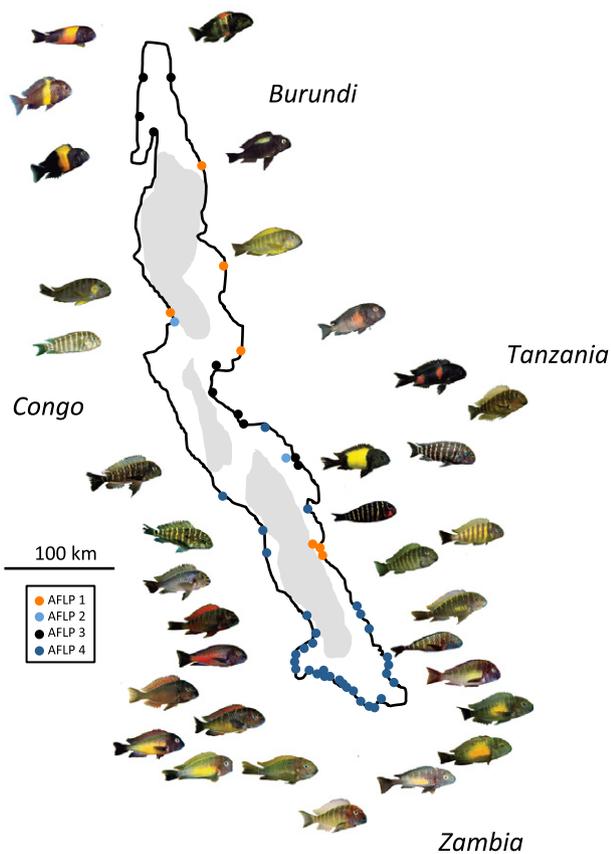
In its early days, the field of speciation was greatly influenced by the search for allopatric situations that would produce the genetic divergence necessary for reproductive isolation (Mayr 1942). Indeed, the description of trans-isthmian geminate fish species in Panama was a key step towards understanding allopatric speciation processes (Jordan 1908). To this day, geminate species are used to calibrate molecular clocks (Bermingham *et al.* 1997; Donaldson & Wilson 1999; Marko 2002; Domingues *et al.* 2005; Lessios 2008). Biogeographical data, where species distributions yield some insight into the speciation process, have been used since the allozyme era (Stepien *et al.* 1994), soon followed by studies based on mtDNA markers (Avice 1992; Grant & Bowen 1998; Bowen *et al.* 2001). Yet, biogeographical data based on species-level approaches can only give a very coarse idea of the speciation process. These approaches were, in turn, replaced by within-species-level studies, the realm of phylogeography (Avice 2000). An entire field of investigation started and is still active, where an explicit geographical component is combined with genetic data to identify the potential for abiotic factors to play a role in various biotic processes, including speciation (Rocha & Bowen 2008; Puritz *et al.* 2012; Andrew *et al.* 2013). For marine fishes, biogeographical boundaries were seen as the potential nexus of population genetic discontinuities (Dawson 2001; von der Heyden *et al.* 2011), be it the large expanse of open water between the western and eastern Pacific Ocean (Lessios & Robertson 2009), the somewhat permeable southern tip of the Baja California Peninsula (Present 1987; Terry *et al.* 2000; Huang & Bernardi 2001; Bernardi *et al.* 2003; Schinske *et al.* 2010), the stretched Hawaiian Archipelago (Ramon *et al.* 2008; Craig *et al.* 2010; Eble *et al.* 2011), the Mona Passage in the Caribbean Sea (Shulman & Bermingham 1995; Taylor & Hellberg 2006) or the complex Indo-West Pacific (Messmer *et al.* 2005; Drew & Barber 2012; Gaither & Rocha 2013). Physical boundaries that limit gene flow are mostly absent in marine systems, and an interplay between dispersal capabilities, via long PLDs, and oceanic currents was suggested as the main cause for incipient speciation and the subject of further research (Weersing & Toonen 2009; White *et al.* 2010; Faurby & Barber 2012). Several studies specifically investigated the relationship between PLD and

gene flow with mixed results (Waples 1987; Doherty *et al.* 1995; Shulman & Bermingham 1995; Riginos & Victor 2001). However, the lack of a simple correlation between PLD and gene flow was attributed, at least in part, to theoretical and technical limitations (Weersing & Toonen 2009; Faurby & Barber 2012).

The next step was to better assess and understand the role of larval movement in marine fishes. The unexpected discovery of high levels of self-recruitment in coral reef fishes in the late 1990s (Jones *et al.* 1999; Swearer *et al.* 1999) prompted the use of microsatellites and paternity analyses to identify the path of individual fish larvae (Jones *et al.* 2005; Almany *et al.* 2007; Saenz-Agudelo *et al.* 2009; Bernardi *et al.* 2012a,b; Berumen *et al.* 2012; Harrison *et al.* 2012). These studies showed, for the first time, that coral reef fish larvae may not travel far from their natal grounds, resulting in great potential for reduced gene flow, philopatry and local adaptation. These results ultimately reconciled the apparent paradox between the lack of physical barrier in the ocean, theoretically preventing allopatric speciation, and high species diversity in coral reefs. Reduced gene flow and assortative mating, evoked to explain the population structure of *Acanthochromis polyacanthus*, an apelagic damselfish, were also consistent with these results (Planes & Doherty 1997; Planes *et al.* 2001; Van Herwerden & Doherty 2006).

In general, freshwater bodies tend to be relatively small, thus providing limited possibility for spatial differentiation, diversity of ecological niches and ultimately speciation. Indeed, a quest to find allopatric isolation within a body of water was not as developed in freshwater systems for two main reasons (Puebla 2009). First, the larvae of freshwater fishes tend, in general, not to be transported over long distances by currents, because most freshwater species do not have dispersive larvae. Second, it is rare to find semi-permeable boundaries in freshwater systems. Nevertheless, when possible and relevant, this question has been investigated. For example, glacial cycles in North America created pockets of allopatry that produced large numbers of freshwater fish species and were characterized as 'speciation pumps' (April *et al.* 2013a,b). Another classic example is the rise and fall over geological times of the water level in Lake Tanganyika that resulted in almost complete physical separation of smaller bodies of water within the lake, eventually leading to allopatric genetic divergence for populations of cichlids trapped in those isolated pools. These were later rejoined when water levels rose again, the secondary contact completing the speciation process (Sturmbauer & Meyer 1992). This was shown in both rock-dwelling and open-water cichlids, including the spectacular case of the rock-dwelling *Tropheus* using amplified fragment

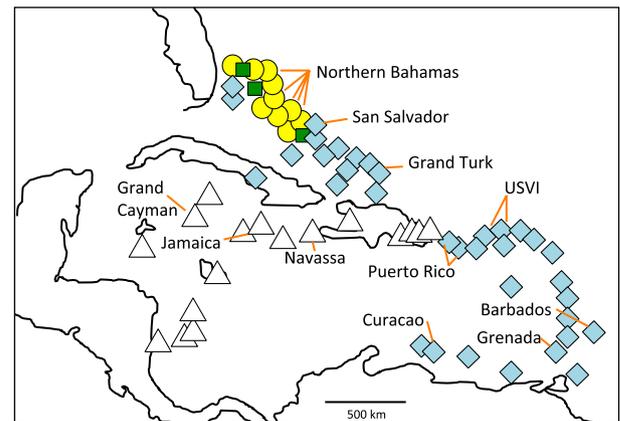
length polymorphism (AFLP) data, where allopatric situations due to water level fluctuations resulted in more than 100 populations and sister species (Egger *et al.* 2007; Fig. 1). Similarly, allopatric situations emerged due to the high flow of large rivers, such as the Amazon or the Congo, which are essentially impassable for most fishes, and are just as effective a barrier to gene flow as a hard physical boundary (Albert & Crampton 2010; Lundberg *et al.* 2010; Markert *et al.* 2010). Indeed, the Amazon outflow on the coast of Brazil is so powerful that it also greatly influences speciation in marine species (Rocha 2003). For freshwater fishes, where river drainages provide physical boundaries, the focus shifted to the historical component of freshwater drainages that over time shifted their locations or resulted in captures (Burrige *et al.* 2006). In Africa, for example, plate tilting was shown to play an essential role in river captures resulting in fish speciation (Giddelo 2002; Hermann *et al.* 2011; Koblmüller *et al.* 2012; Musilová *et al.*



**Fig. 1** Map of Lake Tanganyika showing colour morphs diversity of cichlids in the genus *Tropheus*. Deep-water basins of the lake are represented with grey shading. The dots marking sampling sites were colour-coded to show the distribution of the four major AFLP clades. Note the genetic divergence as it relates to allopatric distribution at low-water levels. Redrawn from Egger *et al.* (2007).

2013). In North America, the freshwater darters (genus *Percina*) are a case in point, where allopatric speciation resulted in more than 50 species among river systems found on the eastern continental divide of the United States (Near *et al.* 2011).

While geographical isolation, in itself, does eventually result in speciation, the mechanisms of reproductive isolation do not follow a single mode. The simplest one, at the mechanistic level, is drift, where in due time markers become fixed by chance alone ( $n$  or  $4n$  generations in populations of  $n$  individuals, for mitochondrial and nuclear markers, respectively; Avise 2004). In this case, for accurate estimation of drift, markers must be neutral. Yet, more complex and realistic scenarios involve situations where assortative mating, reduced gene flow and local adaptation, which are in direct violation of Hardy–Weinberg equilibrium requirements, all play an important role in creating reproductive barriers (Puebla *et al.* 2012). For example, in livebearing fishes of the genus *Poecilia*, independent invasion of extreme habitats (sulphide springs) repeatedly resulted in local adaptation leading to speciation (Tobler *et al.* 2011; Kelley *et al.* 2012; Plath *et al.* 2013). In general, these situations are much more complex to assess genetically, and the power of few mitochondrial, or nuclear loci, is usually insufficient (thus, the prevalence of neutral studies in the literature). The use of thousands of single nucleotide polymorphisms (SNPs), once difficult to obtain, has recently become reachable with the advent of massively parallel sequencing (MPS) and has efficiently been used in both marine and freshwater systems (Hohenlohe *et al.* 2010a; Seeb *et al.* 2011; Puritz *et al.* 2012). In sticklebacks,



**Fig. 2** Distribution of the yellow (circles), blue (diamonds) and white (triangles) forms of the reef goby *Elacatinus evelynae* across the Bahamas and Caribbean Sea. Green squares indicate localities where both blue and yellow forms have been reported. The 17 localities that were sampled by Taylor & Hellberg (2003) are indicated with orange lines. Redrawn from Taylor & Hellberg (2003).

isolation of populations during the last glaciations and evidence of local adaptation have both been shown using RAD sequencing (Hohenlohe *et al.* 2010a,b).

### Ecological component

Early work on the ecological component of speciation in fishes focused on feeding competition, resource partitioning and character displacement (Fryer & Iles 1972). The ecological guild of marine surfperches (Embiotocidae) in California, for example, was described as a small flock with partitioned resources (Ebeling & Laur 1986). In some cases, such as the separation of the closely related black surfperch, *Embiotoca jacksoni* and striped surfperch, *E. lateralis*, morphological differences in the feeding apparatus (the musculature of the pharyngeal jaws) allowed winnowing (sorting food within the mouth; *E. jacksoni*), or not (*E. lateralis*), resulting in competition disequilibrium (Drucker & Jensen 1991). It is within this context that studies on feeding specialization and fish species flocks were set. Species flocks have been studied in few marine systems, such as the rockfishes in California (genus *Sebastes*), the notothenes in the Antarctic, the South African clinids and the New Zealand triplefins (Johns & Avise 1998; Alesandrini & Bernardi 1999; Hickey *et al.* 2009; von der Heyden *et al.* 2011; Janko *et al.* 2011). In contrast, literature on freshwater systems abounds. Extinct species flocks of semionotid fishes (related to the extant gars) have been described from ancient Mesozoic freshwater rift lakes within continental North America (McCune 2004), where both spatial and temporal fossil series are available (McCune *et al.* 1984), so the phenomenon of adaptive speciation within a lake is not new. Yet the study of current situations helped clarify some key questions as to the mechanisms of speciation within a confined environment. This started with the seminal study by Fryer and Iles on the cichlid species flocks of the Great Lakes of Africa (Fryer & Iles 1972), followed by the discovery of other, more reduced, species flocks such as the *Cyprinodon* pupfishes in the Yucatan Peninsula (Humphries & Miller 1981), the barbs of lake Tana, Ethiopia (Nagelkerke *et al.* 1994), the sculpins of Lake Baikal (Kontula *et al.* 2003) and the sailfin silversides of the Malili Lakes, Sulawesi (Herder *et al.* 2006). Niche partitioning and feeding mechanisms were a major focus, and indeed feeding specialization followed by reproductive isolation is central to ecological speciation in fish species flocks (Barlow 2000; Nosil 2012) and not unlike what is observed in Darwin's finches (Grant & Grant 2006; Rands *et al.* 2013). Cichlid flocks that evolved independently in the Great African Lakes (Meyer *et al.* 1990; Verheyen *et al.* 2003; Sturmbauer *et al.* 2011; Loh *et al.* 2013) belong together with the

wrasses and damselfishes to the Ovalentaria, a group of fish with highly developed and specialized pharyngeal jaws (Wainwright *et al.* 2012; Betancur *et al.* 2013; Near *et al.* 2013). With more than 500 species found within a single lake (Lowe-McConnell 1994), early morphological work on feeding specializations begat the search for developmental genes responsible for the origin of morphological differences in pharyngeal jaws, a proxy to understand the underpinnings of ecological speciation via feeding specialization in this group (Albertson *et al.* 2003). Yet, the mechanisms of speciation within a lake are the result of several interconnected factors, divergent selection on feeding types being just one of them. Indeed, besides the well-known cichlids, other, nonlabroid species, such as Mastacembelid eels and *Synodontis* catfish also show adaptive radiation in those lakes, albeit in lesser numbers (Day & Wilkinson 2006; Brown *et al.* 2010; Wright 2011). To tease out the various factors involved, much simpler systems were sought.

The ecological component may be evaluated in its simplest form, when only two ecotypes are found. In that situation, ecological speciation occurs as a result of the adaptation to two different environments, later followed by secondary contact and reproductive isolation (with reinforcement if hybrids exhibit lowered fitness; Rundle & Schluter 2004). A perfect case scenario was found in three-spined sticklebacks (*Gasterosteus aculeatus*), a species complex that is found both in freshwater and in coastal marine environments of the higher latitudes in the northern hemisphere. In postglacial freshwater lakes in British Columbia, Canada, two sympatric forms are present, a limnetic form that specialized on plankton feeding and a benthic form that feeds primarily on benthic invertebrates, the primary source of their ecological divergence (Schluter & McPhail 1992; Schluter 1993). They consequently show differences in their shape and in particular in their gill rakers, which are comb-like structures used to trap food and most developed in planktonic feeding forms. This situation arose independently several times, suggesting similar evolutionary constraints and thus becoming a very clear and simple model for parallel evolution, adaptive radiation and ecological speciation (Nagel & Schluter 1998; Schluter 2000; McKinnon & Rundle 2002; but see Ishikawa *et al.* 2013). With the sequencing of more than 20 stickleback genomes and population-level genome scans (RAD sequencing), the genomic regions under selection were recently identified (Hohenlohe, *et al.* 2010a; Jones *et al.* 2012). Importantly, the limnetic-benthic model goes beyond sticklebacks. It was found in other systems, mostly in North American glacial regions (Taylor 1999), such as the lake whitefish (*Coregonus clupeaformis*; Gagnaire *et al.* 2013), but also in the Neotropical Midas cichlid species complex (Muschick *et al.* 2011).

The stickleback system fits the ecological speciation model, yet it does not require sympatry, at least not in its first stage, because in this model, adaptation to different environments may occur in allopatry. Indeed, it has been suggested that the limnetic form may be genetically more closely related to marine populations than to the benthic form, thus indicating that sympatric speciation within each lake may not be the most parsimonious explanation. Thus, the possibility of sympatric speciation was tantalizing but still contentious.

Where situations are more complex than the simple limnetic–benthic dichotomy, more than two species are observed (Østbye *et al.* 2006), and ultimately when the size of the body of water and the diversity of potential ecological niches are great, then species flocks may emerge, as is the case for Great African Lake cichlids (Sturmbauer *et al.* 2011). At the macroscopic scale, where phylogenies may be seen as evidence of speciation past (Barraclough & Nee 2001), early work suggested that the cichlid species flocks found in the Great African Lakes had evolved within each lake, thus sympatric speciation in some groups was a likely explanation (Meyer *et al.* 1990; Verheyen *et al.* 2003; but see Loh *et al.* 2013). In simpler situations, cichlids offered better situations to test for sympatric speciation, namely in Cameroon's and Nicaragua's crater lakes (Schliewen *et al.* 1994, 2001; Barluenga *et al.* 2006a). In the latter case, a combined morphological, ecological, phylogeographical and genetic approach provided convincing evidence that sympatric speciation had occurred in the Midas cichlid (*Amphilophus sp.*) species complex in Lake Apoyo, Nicaragua (Barluenga *et al.* 2006a), a claim that resulted in some debate (Barluenga *et al.* 2006b; Schliewen *et al.* 2006). In marine systems, evidence for sympatric speciation is much more difficult to assess. In the Neotropical reef gobies in the genus *Elacatinus*, where about 30 species are found around the Isthmus of Panama, no sister relationships were found across the Isthmus (geminant species); instead, all sister relationships were found within an ocean basin (Taylor & Hellberg 2005). Genetic differences instead matched ecological and coloration patterns and were suggestive of sympatric speciation (Fig. 2; Taylor & Hellberg 2003, 2005, 2006). Coyne & Orr (2004) defined four criteria needing to be fulfilled for sympatric speciation to be inferred: a sympatric distribution, a monophyletic sister species relationship, an ecological setting where allopatric speciation is unlikely, such as a crater lake of recent origin as described above, and complete reproductive isolation. The latter condition, however, needs to be qualified because more recent speciation concepts specifically do not require reproductive isolation (Hausdorf 2011). For greenling from Japan (genus *Hexagrammos*), where these conditions are met (except for

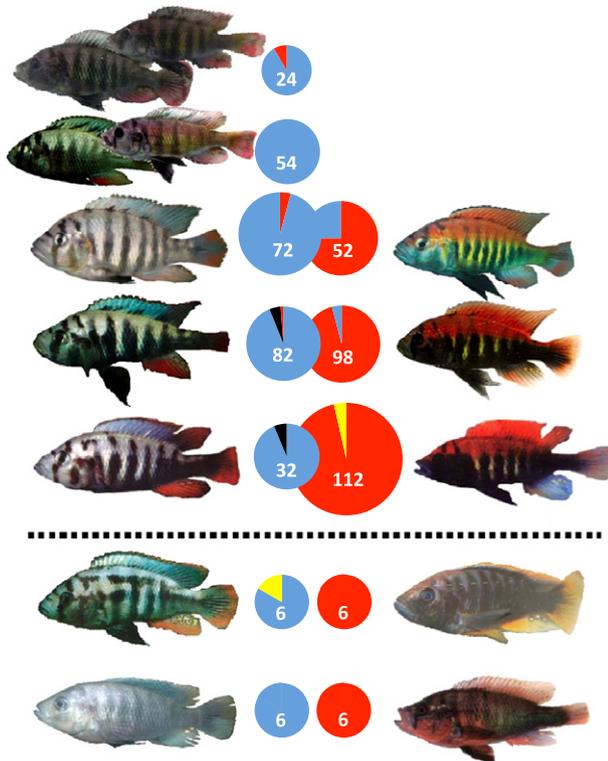
reproductive isolation), a combination of experiments and fitness levels of artificial crosses were tested, thus providing a solid case for sympatric speciation in marine fishes (Crow *et al.* 2010).

### Sexual component

Studies that focus on the sexual component of speciation have steadily been increasing in the past few years (Coyne & Orr 2004). In fishes, male courtship translates primarily in behavioural displays and coloration signals. Where water is naturally turbid, male display may take unusual forms. One spectacular example is found in West Africa's mormyrid elephant fishes that use weak electric fields generated by muscular contractions to assess their environment and feed. There, an entire species flock is the result of sexual selection on male electric displays (Sullivan *et al.* 2002; Arnegard *et al.* 2010). In clear water, the most prominent aspect of male display involves reflection and coloration (Maan *et al.* 2010). Indeed, when clear water becomes turbid due to unnatural alterations, as was the case in Lake Victoria following the introduction of the Nile perch (which required smoking as opposed to the traditional drying of smaller cichlid fishes, thus leading to deforestation and the subsequent soil runoff), break down of assortative mating resulted in rampant hybridization and its associated loss of diversity in local cichlids (Goldschmidt 1996; Seehausen 1997).

Divergent selection on sensory systems may cause speciation through sensory drive. This is observed when female sensory bias plays a role in initiating the process of a given display as was shown in swordtails (genus *Xiphophorus*), where females select large colourful swords (Meyer 1997; Rosenthal & Evans 1998). For mouthbrooding haplochromine cichlids, high speciation rates were presumed to be driven by sensory bias where females are attracted to egg spots (egg-shaped markings in the males' anal fin), but experimental work determined that this was unlikely (Henning & Meyer 2012). In contrast, female sensory bias for particular male nuptial colours was theoretically predicted, modelled and observed in Lake Victoria (Maan *et al.* 2006; Kawata *et al.* 2007; Seehausen *et al.* 2008). A correlation was found between the colour of *Pundamilia* cichlids (red or blue) and their visual pigments (opsin genes; Carleton *et al.* 2005). There, opsins are first adapted to different shallow- and deep-water light environments with their respective H and P alleles. Allele H is most associated with red male nuptial display, while the P allele is mostly associated with the blue phenotype. Males specifically display in wavelengths that are best seen by females, resulting in assortative mating pairs, and eventually speciation is the outcome of sensory

drive. The predicted replicated blue/red species pairs were observed several times in the *Pundamilia* species complex (Seehausen *et al.* 2008; Terai & Okada 2011; Fig. 3). Expectedly, mate choice based on male coloration is a way to rapidly create reproductive isolation (Wagner *et al.* 2012). The resulting assortative mating has been widely observed directly or indirectly (using genetic signatures), in both marine and freshwater fishes (Knight & Turner 2004; Puebla *et al.* 2007, 2012;



**Fig. 3** The male nuptial phenotypes and long-wave sensitive opsin (LWS) allele group frequencies of all studied sympatric species and population pairs of *Pundamilia*. The hatched line separates the *P. pundamilia*/*P. nyererei* complex from other species pairs. Left column: blue types, right column: red dorsum and red chest types. From top: representative males of blue and reddish phenotypes in the variable but predominantly blue *Pundamilia* population from Marumbi Island; representative males of blue and reddish phenotypes in the variable but predominantly blue *Pundamilia* population from Luanso Island; representative males of the blue and red incipient species from Kissenda Island; representative males of the blue and red incipient species from Python Island; representative males of *P. pundamilia* and *P. nyererei* from Makobe Island; representative males of *P. pundamilia* and *P. igneopinnis* from Igombe Island; representative males of *P. azurea* and *P. sp.* 'red head' (red chest type) from Ruti and Zue islands respectively, these species are sympatric and syntopic at Mabibi Islands, situated between Zue and Ruti Islands. Numbers in the allele frequency pies are the number of haplotypes sequenced. From Seehausen *et al.* (2008).

Blais *et al.* 2009; Leray *et al.* 2010; Smadja & Butlin 2011). For example, at least nine colour morphs of the Caribbean hamlets (genus *Hypoplectrus*) have been observed mating assortatively, as suggested prior to incipient speciation (Fischer 1980; Domeier 1994; Puebla *et al.* 2007, 2012), yet nearly no genetic divergence has yet been found between *Hypoplectrus* morphospecies when using a number of different molecular assays (McCartney *et al.* 2003; Ramon *et al.* 2003; Puebla *et al.* 2007, 2012; Barreto & McCartney 2008).

To fully appreciate the visual environment of fishes, work has been done either at the ecological level, as for the classic case of guppies (Endler 1980; Kodric-Brown 1985), looking at visual pigments (Cummings & Partridge 2001), or by sequencing opsin genes (visual pigments) to indirectly elucidate visual potential driven by sexual selection, as mentioned above and in other cases as well (Carleton *et al.* 2005; Terai *et al.* 2006; Seehausen *et al.* 2008; Miyagi *et al.* 2012). The more difficult task of identifying the genes responsible for display coloration was achieved by looking at differential expression in transcriptomes of divergent colour morphs of the Midas cichlid (Henning *et al.* 2013).

An intriguing case of potential runaway selection was uncovered in species of Lake Malawi mbuna (rock-dwelling) cichlids. Ecological and molecular mapping work was done on a colour morph, orange blotch (OB), which is predominantly found in females in both Lake Malawi and Lake Victoria (Streelman *et al.* 2003; Ser *et al.* 2010). Recently, the situation became more complex because the interest in coloration and mating shifted to the issue of sexual conflicts. In this context, speciation may occur through the interplay of assortative mating, sexual conflict and colour patterns (Kocher 2004; Parnell & Streelman 2013). What was unexpected was that the OB colour was found to be linked with the ZW female sex-determining locus (found on chromosome 5), and the blue nuptial colour pattern was linked with two XY male sex-determining loci found on two different chromosomes (Parnell & Streelman 2013). Thus, this system is a perfect setup for a role of 'polygenic sex-determining systems in rapid evolutionary diversification' (Parnell & Streelman 2013). This system may explain both the high diversification of Great African Lake cichlid flocks and its unusual fast rate.

As discussed above, prezygotic isolation via assortative mating is well documented in fish. The fertilization stage has also been an important topic of investigation as it relates to potential for reproductive barriers. The study of the fast-evolving gamete recognition proteins is key to understanding speciation in marine invertebrates (Vacquier 1998; Palumbi 2009); yet, little is known about their counterparts in vertebrates in general and in fishes in particular. Zona pellucida, ZP,

glycoproteins, which are represented by at least seven genes in fish, have been sequenced and are good candidates for the egg portion of the equation, but no experimental work has been done to relate genotype, gamete incompatibilities and speciation in fishes (Sun *et al.* 2010). Instead, an indirect measure of sexual conflict and sperm competition has been gathered in a very large number of studies through the evaluation of levels of multiple paternity or multiple maternity (in reversed gender role pipefish and seahorses) in fishes (Jones & Avise 1994; Reisser *et al.* 2009; Coleman & Jones 2011; Liu & Avise 2011). High levels of multiple paternity (intraspecific) and hybridization (interspecific) clearly show that prezygotic isolation at the fertilization stage is not the primary means of reproductive isolation in fishes. In fact, in some cases, hybridization has generated diversity resulting in speciation (Dowling & DeMara 1993; Keller *et al.* 2012). For example, in cases where new ecological niches can quickly be invaded, fitness advantages may be gained by populations where hybridization is common (Seehausen 2004). Following this model, empirical data have been accumulating, showing that this phenomenon, once considered extremely rare, may be more common than once thought (Salzburger *et al.* 2002; Koblmüller *et al.* 2007; Genner & Turner 2012; Ward *et al.* 2012; Cui *et al.* 2013). The general (and likely more common) rule, however, that postzygotic isolation occurs via lowered hybrid fitness (known as the Dobzhansky–Muller model of hybrid incompatibility) has been shown in several examples (Rogers & Bernatchez 2006; Crow *et al.* 2007, 2010; Gagnaire *et al.* 2012a,b; Montanari *et al.* 2012).

### Conclusion—towards a unifying genomic approach

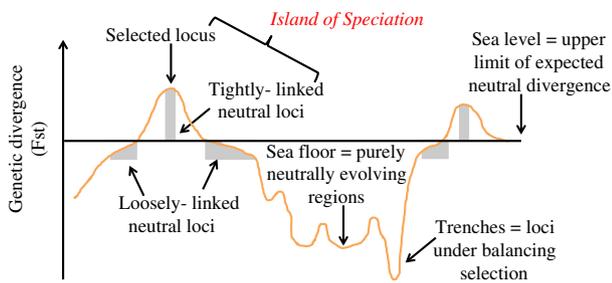
Speciation in different systems tend to result from some predominant factor; yet, artificially separating the different factors that play a role in speciation, as was done above, is to caricature a complex process that has multiple facets. Luckily, it is now possible to take a more comprehensive view of the entire process (Maan & Seehausen 2011). As was shown extensively above, fish present a very diverse array of scenarios, making them an ideal model to study speciation processes. That said, speciation in fishes has constraints that are peculiar to this group. Mating processes that rely on communication have to accommodate the aquatic medium, be it turbid, clear, with or without colour, ultraviolet or polarized light. This in turn will influence female choice and male display, which will drive the strength of assortative mating (Langerhans & Makowicz 2013; Langerhans & Riesch 2013). External fertilization has also resulted in strong potential for prezygotic isolation.

Once fertilized, eggs and larvae generally move freely in the water column and thus influence dispersal, gene flow and the likelihood of breeding incompatibilities via neutral processes.

All these factors have been studied at length, as we have discussed, but mostly in isolation. For technical reasons, trying to understand speciation at the genetic level used to be restricted to the search of a single or few genes that would be the speciation smoking gun. Following the Dobzhansky–Muller (DM) model of hybrid incompatibility, where a gene would bring overall fitness to zero in a hybrid, the melanoma-causing gene *Xmrk-2* in *Xiphophorus* swordtail hybrids, which has also deleterious effects in other fish species, such as medaka, was considered a good speciation gene candidate (Wu & Ting 2004). The recent developments of massively parallel sequencing are now allowing us to have a much more global view of the speciation process. They are bringing together, for the first time, genomic approaches that are unifying the language of speciation (Butlin *et al.* 2012; Gagnaire *et al.* 2013). All the factors influencing speciation leave strong genomic signatures and time is ripe to identify the fundamental molecular mechanisms responsible for these effects (Andrew *et al.* 2013).

In the early phase of speciation, gene flow occurs between two incipient species, which is theoretically an impediment to the genetic diversification necessary to produce a breeding barrier (Kulathinal *et al.* 2009). At the genomic level, however, chromosomal rearrangements and differential recombination will produce differential gene flow levels along the genome (Rieseberg 2001). In the best studied case of recent speciation, humans and chimps, genomic regions that are syntenic (where gene order is maintained in a colinear fashion) show much higher levels of gene flow than regions that are not (Farré *et al.* 2013). These regions are visualized as a local increase in *F<sub>st</sub>* levels and create an opportunity for genetic disruption resulting in speciation, and these regions are often referred to as speciation islands (Nielsen *et al.* 2009; Nosil & Feder 2012; Hemmer-Hansen *et al.* 2013; Fig. 4). Therefore, high recombination would theoretically increase speciation rates. Genomic regions of high recombination were identified either as GC-rich regions or as fragile regions where GC content rapidly changes along the chromosomes (Fullerton *et al.* 2001; Marsolier-Kergoat & Yeramian 2009; Watanabe & Maekawa 2013). In general, fishes tend to be AT rich and homogeneous (meaning with few compositional jumps in their genome; Bucciarelli *et al.* 2002, 2009), suggesting that at the macroscopic scale, speciation rates should be relatively low in fishes.

Within the islands of speciation, it is unclear what may produce breeding barriers. The rapid divergence of



**Fig. 4** Genomic islands of speciation. Schematic illustration of expected patterns of differentiation along a chromosome. Trenches represent regions under balancing selection that may be lower than average neutral loci (O'Farrell *et al.* 2012), sea floor represents purely neutrally evolving regions, and sea level represents a 'neutrality threshold'. Islands are genomic regions exhibiting greater differentiation than expected under neutrality, thereby rising above sea level. Drawing modified from Nosil *et al.* (2009).

regions that experience low levels of gene flow may, in itself, prevent effective reproduction, not unlike the predictions of the DM model of hybrid incompatibility. In that respect, the islands of speciation, which persist in the face of high gene flow, were proposed to contain the genes responsible for reproductive isolation (Turner *et al.* 2005), which would be identified using  $F_{st}$  outlier methods for example (Storz 2005); however, this is clearly not always the case (Macaya-Sanz *et al.* 2011). Instead, reproductive barriers may simply be generated by genetic incompatibilities due to a lack of syntenic regions (Stukenbrock *et al.* 2010), and there should be little difference if the regions are coding or noncoding, yet this remains controversial (Woolston 2013). Admittedly, the presence in those regions of key genes involved in reproduction predicts an increase in speciation rates. Because genes tend to be at higher concentration in GC-rich regions (Bernardi 2000) and those are subjected to higher recombination levels, there may be a link between a higher than expected concentration of genes and the location of speciation islands.

These are exciting times for the field of speciation, because we have new tools to quickly identify large numbers of SNPs and their significance to genetic divergence and speciation (Bernatchez *et al.* 2010; Hohenlohe *et al.* 2012; Krück *et al.* 2013). Vast amount of sequencing is affordable (e.g. Amemiya *et al.* 2013), and analytical tools are available to assess the demographic history of a species using the genomic sequence of very few or even a single individual, thus allowing for probing speciation events from the recent past (Li & Durbin 2011; Miller *et al.* 2012). Yet, as genomic tools become incredibly powerful and affordable, major biological questions remain, and these can only be fully understood in the light of careful examination and understanding of the

actual organism in its natural environment. It is ironic that the mechanisms of speciation are becoming best understood in an era where the environment that promotes speciation is being relentlessly degraded.

## Acknowledgements

I would like to thank my colleagues of the Department of Ecology and Evolutionary Biology at the University of California Santa Cruz for having broadened my biological knowledge over the years, in particular Pete Raimondi, Mark Carr, Grant Pogson, Bruce Lyon, Barry Sinervo and John Thompson. I would like to thank Kendall Clements for numerous discussion on fish ecology and speciation. I would like to thank my father, Giorgio Bernardi, for discussing genome evolution for the better part of the last 30 years. Finally, I would also like to thank the members of my laboratory for their patience, good food and good humour, which makes my daily work most enjoyable.

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