

RESEARCH PAPER

Speciation in marine environments: Diving under the surface

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Abstract

Marine environments are inhabited by a broad representation of the tree of life, yet our understanding of speciation in marine ecosystems is extremely limited compared with terrestrial and freshwater environments. Developing a more comprehensive picture of speciation in marine environments requires that we 'dive under the surface' by studying a wider range of taxa and ecosystems is necessary for a more comprehensive picture of speciation. Although studying marine evolutionary processes is often challenging, recent technological advances in different fields, from maritime engineering to genomics, are making it increasingly possible to study speciation of marine life forms across diverse ecosystems and taxa. Motivated by recent research in the field, including the 14 contributions in this issue, we highlight and discuss six axes of research that we think will deepen our understanding of speciation in the marine realm: (a) study a broader range of marine environments and organisms; (b) identify the reproductive barriers driving speciation between marine taxa; (c) understand the role of different genomic architectures underlying reproductive isolation; (d) infer the evolutionary history of divergence using model-based approaches; (e) study patterns of hybridization and introgression between marine taxa; and (f) implement highly interdisciplinary, collaborative research programmes. In outlining these goals, we hope to inspire researchers to continue filling this critical knowledge gap surrounding the origins of marine biodiversity.

KEYWORDS

demographic history, dispersal, effective population size, gene flow, genomic architecture, geographic isolation, hybridization, interdisciplinary research, natural selection, reproductive barriers

1 | INTRODUCTION

Marine ecosystems harbour an important component of Earth's biodiversity. This is particularly well illustrated at high taxonomic levels, where 16 phyla are unique to the marine realm, whereas only one phylum is unique to terrestrial and none to freshwater environments (Jezkova & Wiens, 2017). Investigating the main processes underlying diversification in marine environments is thus crucial for a more general understanding of the origins and distribution

of biodiversity. The study of how reproductive barriers between marine organisms accumulate resulting in new species in a broadly connected environment is also vital for the long-standing evolutionary debate concerning the importance of isolation by physical barriers in speciation.

During most of the last century, our knowledge about the origin of species in the marine realm was very limited, with the exception of a few taxonomic groups (e.g. sea urchins; Mayr, 1954; Palumbi, 1992, 1994). This was actually stated explicitly by one of

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the most prominent researchers of speciation, Mayr (2001): 'For most animal groups, particularly the marine ones, we have no clues whatsoever what facilitates speciation. Here even the nature of the separating barriers between different water masses is unknown'.

There are several reasons for this knowledge gap. First, the study of speciation in the sea/ocean is inherently challenging. For example, sunlight usually penetrates only tens of metres below the water's surface. Thus, despite recent technological advances we still heavily rely on echo sounding, or destructive methods such as trawling, to map many marine habitats on the seafloor, which provides a very incomplete picture of the existing diversity. Consequently, most of the seascape remains uncharacterized. Second, the number of laboratories with resources to conduct expensive and time-consuming surveys, including access to research vessels and submersible vehicles, is also limited. Third, it is difficult to complete the life cycle of many marine organisms in the laboratory, impeding the creation of lines, the implementation of crosses and the quantification of reproductive isolation, all of which are important tools in speciation research. Additionally, manipulative experiments in the field or the study of hybrid zones are very challenging for many marine organisms, further limiting the study of reproductive barriers *in situ*. Finally, unlike a few specific biogeographic regions such as the Baltic Sea or the Isthmus of Panama (Andr n et al., 2011; Knowlton et al., 1993), vast areas of our oceans remain poorly characterized, limiting our knowledge of the geographic and demographic history of speciation in the sea. Thus, it is no surprise that a more complete knowledge about speciation in marine organisms comes from a limited number of taxa, including rocky shore snails (Johannesson et al., 1995), rock pool copepods (Ellison & Burton, 2008), Atlantic cod and anadromous freshwater forms of three-spined sticklebacks (Barth et al., 2019; Jones et al., 2012), killer whales (Foote et al., 2016) and *Prochlorococcus* cyanobacteria (e.g. Johnson et al., 2006).

Despite pointing out the need for a better understanding of the nature of isolating barriers between most marine species, Mayr was a keen proponent of the importance of allopatric speciation, both in terrestrial and marine environments. Supported by early work on sea urchins (Mayr, 1954), he championed the idea that geographic isolation was the main driver of speciation in the sea—a view that prevailed for several decades (Palumbi, 1992). Most marine organisms have high dispersal, with passive drift of larvae and/or adults by ocean currents over large distances, which may prevent differentiation across extensive marine areas. Thus, students of marine speciation were faced with a well-known paradox: if most speciation in the sea is allopatric, how can new species form in the absence of complete geographic barriers (Johannesson, 2009)?

The observation of extensive hybrid zones between closely related species further suggested that marine speciation could occur without complete geographic isolation (Bierne et al., 2003). This includes cases where gene flow occurred during the entire speciation process (primary differentiation) and/or after an initial period of geographic isolation (secondary contact); hereafter we refer to all these cases as 'speciation with gene flow' for convenience. Together with the identification of many different reproductive barriers between

closely related marine species, including the existence of gamete recognition mechanisms (Palumbi, 1994; Swanson & Vacquier, 1998), habitat choice and asynchronous spawning (Bierne et al., 2003), this caused a paradigm shift in marine speciation research. As a consequence, the number of examples of speciation with gene flow in marine environments has been increasing (reviewed by Potkamp & Fransen, 2019). Despite these advances, our knowledge about speciation is still largely biased towards terrestrial organisms (figure 1 in Miglietta et al., 2011).

Benefiting from recent technological advances in different fields, from maritime engineering to genomics, we now have access to increasingly large biological and environmental data sets from the oceans, including areas or habitats that were previously inaccessible such as the deep sea (Costa et al., 2020). This offers an unprecedented opportunity to characterize the main reproductive barriers and evolutionary mechanisms underlying speciation of marine life forms across multiple ecosystems and taxa, and to provide a more complete view of speciation across a diverse range of marine environments. Inspired by the discussions during a symposium of the international *Marine Evolution* conference in Sweden organized in 2018 by the Linnaeus Centre of Marine Evolutionary Biology, University of Gothenburg, we compiled this special issue containing 14 contributions on current research progress on speciation in marine environments.

This editorial piece highlights some of the main findings of these contributions. We propose six main research axes that we think will move the field forward, resulting in a more comprehensive and balanced knowledge about the origin of species in the sea: (a) studying speciation across more diverse marine ecosystems and a broader phylogenetic range of organisms; (b) identifying the full diversity of reproductive barriers between species in diverse marine ecosystems; (c) understanding the role of different genomic architectures in promoting reproductive isolation between closely related marine species; (d) inferring the evolutionary history of divergence using model-based approaches; (e) studying hybridization and introgression especially in marine hybrid zones; and (f) implementing integrative interdisciplinary research, to establish a better link between genotypes, phenotypes and the environment, and to understand how their interaction drives speciation in marine organisms.

Ultimately, we hope that this special issue helps to inspire future research programmes to address key evolutionary questions in speciation research, such as: Is there a qualitative or quantitative difference between the mechanisms and rates of speciation in marine, terrestrial and freshwater ecosystems? What can we learn about speciation by specifically studying marine organisms? What are the main differences between the prevailing reproductive barriers and evolutionary processes involved in speciation across different marine environments?

2 | DIVING UNDER THE SURFACE

Before trying to answer these questions, perhaps one should first ask what the main reasons are for hypothesising that there may be something unique about speciation in marine environments?

On one hand, it could be argued that the types of (post-zygotic or prezygotic) reproductive barriers and processes involved (natural selection, sexual selection, drift, etc.) should be the same in marine, terrestrial and freshwater ecosystems. However, it is often argued that populations of many marine species show higher connectivity due to the prevalence of pelagic free-swimming or planktonic stages and fewer dispersal barriers than in most terrestrial and freshwater environments (e.g. Palumbi, 1992; Puebla, 2009). Furthermore, many marine species tend to have large effective population sizes, which may impact speciation in two ways. First, theory suggests that larger populations should contain higher levels of genetic diversity, meaning that more genetic variation is available to fuel speciation. Second, selection—including divergent selection that opposes gene flow between taxa—is expected to be more effective in larger populations (Barrio et al., 2016). However, the relationship between population size and adaptation is probably not as simple as commonly thought (Galtier, 2016; Lourenço et al., 2013). Thus, it is not clear whether speciation with gene flow should be more common in marine than in terrestrial environments. Moreover, this expectation will inevitably differ among taxa. Lower divergence and speciation rates are expected in marine species with long-lived larval dispersal stages than in species with brief larval dispersal phases or with direct development. It would therefore be important to investigate beyond some initial attempts (Bierne et al., 2016) whether selection is more powerful in marine species with large population sizes associated with particular characteristics of the ecosystem, reproductive strategies and/or taxonomic

group. We next discuss some research directions that we think are needed to fill these knowledge gaps.

2.1 | Studying speciation across diverse marine ecosystems and taxonomic groups

Among the broad representation of biodiversity that is available in the sea, most of our knowledge on marine speciation is derived from a small and biased fraction of organisms and ecosystems (Miglietta et al., 2011; Potkamp & Fransen, 2019; Rocha & Bowen, 2008). In part, this is because some marine ecosystems or groups of organisms are much more accessible than others. This is well illustrated in this special issue, where the majority of the contributions target common organisms inhabiting the intertidal realm (Table 1). The geographic coverage of marine speciation studies is also uneven, with the circumpolar regions traditionally underrepresented, despite recent findings suggesting higher speciation rates at high latitudes, at least in fishes (Rabosky et al., 2018). Even for the best studied ecosystems and geographic regions, the number of extant marine species is likely underestimated. After generalized access to molecular markers in the 1980s, many cryptic species were revealed (e. g. Knowlton et al., 1993; Laakkonen et al., 2021), and this number is expected to increase even further with the advent of environmental DNA metabarcoding studies (Holman et al., 2019).

In addition, our general knowledge about the history and distribution of marine species is strongly biased towards marine

TABLE 1 Manuscripts published in this special issue, with information about the focal taxa, type of environments and focal geographic/oceanographic region for each study

Reference	Taxa	Environment(s)	Geographic; oceanographic regions
Berdan et al. (2021)	Fish: killifish	Marine/freshwater	North America; North Atlantic
Choo et al. (2021)	Molluscs: shelled pteropods	Open ocean	Atlantic
Costa et al. (2021)	Mammals: bottlenose dolphins	Coastal/offshore	South America; South Atlantic
Galindo et al. (2021)	Molluscs: flat periwinkles	Rocky intertidal	Europe; North Atlantic
Prada and Hellberg (2021)	Cnidarian: corals	Shallow/deep reefs	North America; North Atlantic, Caribbean Sea
Hudson et al. (2021)	Tunicates: sea squirts	Rocky intertidal/subtidal	Africa; South Atlantic, Indian Ocean
Kess et al. (2021)	Molluscs: rough periwinkles	Rocky intertidal	Europe; North Atlantic
Laakkonen et al. (2021)	Mammals, Molluscs, Fish, Crustaceans, Polychaetes, Echinoderms	Multiple	Europe, North America, Northeast Asia; North Pacific, North Atlantic, Arctic Ocean
Leder et al. (2021)	Fish: gobies	Marine/brackish	Europe; North Atlantic, Baltic Sea
Popovic et al. (2021)	Molluscs: <i>Mytilus</i> mussels	Rocky intertidal	Europe, North America, Africa and Oceania; Atlantic, Pacific, Mediterranean and Tasman Sea
Ravinet et al. (2021)	Fish: sticklebacks	Marine/brackish/freshwater	Asia; North Pacific, Japan Sea
Ribardi�ere et al. (2021)	Crustaceans: isopods	Rocky intertidal	Europe; North Atlantic
Simon et al. (2021)	Molluscs: <i>Mytilus</i> mussels	Rocky intertidal	Europe and North America; North Pacific, North Atlantic, Mediterranean, North Sea, Baltic Sea and Black Sea
Tatarenkov et al. (2021)	Fish: killifish	Mangrove	North America; North Atlantic, Caribbean Sea

vertebrates, such as fish and mammals. Although Mollusca is the phylum with the highest number of marine species, information about genetic divergence and speciation in marine molluscs is limited to a few very common and easily accessible species. For example, mussels of the genus *Mytilus* form a complex system with multiple hybrid zones between various species that have been intensively studied (Bierne et al., 2003; Popovic et al., 2021; Simon et al., 2021). Another taxon that has become a model in the study of ecotype evolution and ecological speciation comprises the gastropods of the genus *Littorina* (Galindo et al., 2021; Johannesson, 2015; Kess et al., 2021; Stankowski et al., 2020; Westram et al., 2018). Some species of corals, seaweeds, seagrasses or sea squirts have also been important targets for studies focusing on genetic divergence and species evolution (Monteiro et al., 2016; Olsen et al., 2004; Pereyra et al., 2013; see also Hudson et al., 2021; Prada & Hellberg, 2021), as have a few species of microalgae and bacteria (Johnson et al., 2006). Although it is not possible to represent all major groups of marine organisms in this special issue, it actually covers notable taxonomic breadth, including fish, molluscs, mammals, polychaetes, echinoderms, cnidarian, tunicates and crustaceans, although we regret plants and algae are lacking (Table 1). This organismal, geographic and ecological bias makes it impossible to establish general principles of speciation that are independent of ecosystem, life-history characteristics and taxonomic position. Therefore, further studies covering a wider range of organisms and ecosystems are needed before we can reach more general conclusions about main patterns and processes of speciation in marine environments.

2.2 | Identifying the main reproductive barriers between marine species

Geographic isolation was initially considered the main factor driving speciation in marine organisms. Thus, our focus on understanding the factors promoting the evolution of reproductive barriers under gene flow is relatively recent (Bierne et al., 2003; Palumbi, 1994; Swanson & Vacquier, 1998). However, examples of speciation with gene flow have become more common, including many cases where ecology plays an important role (reviewed by Potkamp & Fransen, 2019). Despite these advances, systems for which reproductive barriers have been well-characterized remain scarce (as notable examples, see *Littorina saxatilis*: Johannesson, Zagrodzka, et al., 2020; Perini et al., 2020; Westram et al., 2018; *Mytilus* spp.: Bierne et al., 2003; Bierne, 2011; sticklebacks: Jones et al., 2012; Lackey & Boughman, 2016; sea urchins: Lessios, 2007; *Lucania* killifish: Berdan et al., 2021). Oceans are far from being a homogenous mass of water where environmental conditions are constant across space and time. Moreover, they are so big that even with wide dispersal there is opportunity for selection to overcome gene flow. Thus, detailed characterization of environmental parameters with ecological relevance (e.g. salinity, temperature and depth) is needed to understand how natural selection contributes to reproductive isolation, both directly, via habitat or allochronic isolation, immigrant inviability (prezygotic isolation) or extrinsic post-zygotic isolation,

and indirectly, via reinforcement (Berdan et al., 2021; Butlin, 1987; Smadja & Butlin, 2011).

Hybrid zones are particularly informative about the spatial distribution of genotypes and phenotypes in relation to environmental gradients (e.g. Johannesson et al., 2020; Westram et al., 2018) (also, see Section 2.5). Although not very frequent, detailed studies of hybrid zones in marine environments have provided important information about the role of local adaptation in speciation (Kess et al., 2021; Leder et al., 2021; Prada & Hellberg, 2021; Westram et al., 2018), the presence of genetic incompatibilities (Simon et al., 2021) or the coupling between these two types of barriers (Bierne, 2011). Extensive mixing in hybrid zones may also make it possible to identify candidate SNPs or genomic regions underlying reproductive barriers through genome-wide association tests (Duranton et al., 2020).

The genetic and phenotypic characterization of populations associated with different habitats (Costa et al., 2021) also offers insights about the role of divergent selection in speciation with gene flow. Evidence is strongest when it comes from studies of parallel divergence, where multiple populations have diverged due to similar selection pressures at several geographic locations (Galindo et al., 2021; Jones et al., 2012; Morales et al., 2019). Field transplants between different habitats and/or laboratory experiments also provide crucial information about the contribution of environmental selection relative to other barriers such as intrinsic incompatibilities (Berdan et al., 2021; Prada & Hellberg, 2013). The role of behavioural isolation and sexual selection in speciation is perhaps more difficult to study in many marine organisms (but see Barth et al., 2019; Perini et al., 2020). Although for some fish species it is obvious that homing and habitat choice have profound roles in speciation (e.g. Barth et al., 2019), information remains limited for most taxa (but see Berdan et al., 2021; Costa et al., 2021; Ravinet et al., 2021, for a possible role of habitat isolation). In this special issue, two contributions tried to fill this gap. A study using intertidal isopods by Ribardi re et al. (2021) evaluated the role of mate choice in the laboratory showing that sexual selection at least partially contributes to reproductive isolation between two diverging species (*Jaera albifrons* and *J. prae-hirsuta*). The authors suggest that the role of sexual selection in reproductive isolation is independent of ecological isolation. Similarly, behavioural isolation seems to contribute to reproductive isolation between two killifish species (*Lucania parva* and *L. goodei*), even though it was not possible to identify whether this was mediated by female preference and/or male courtship performance (Berdan et al., 2021).

Finally, although the view that geographic isolation plays the main role in speciation in marine environments is losing strength, this does not mean that vicariance or physical barriers are not important in facilitating the evolution of reproductive isolation (Hodge & Bellwood, 2016). Oceans are highly connected environments, but there are still opportunities for allopatric differentiation. Indeed, studies of population differentiation in multiple marine species using genetic markers have suggested that there might be more spatial barriers than previously envisioned (Miglietta et al., 2011). This is

especially true for organisms that release their gametes into the water as well as those with passive larval or adult dispersal. The contribution by Laakkonen et al. (2021) highlights the influence of vicariance in shaping diversification of European amphiboreal marine organisms. Together with geographic barriers, currents may play a major role in population divergence in the oceans (Choo et al., 2021; van der Ven et al., 2020), similar to the role of wind for dispersing seeds of terrestrial plants. Thus, the comparison of patterns of dispersal predicted from biophysical models with those inferred from genetic data allows us to understand how currents influence speciation in the sea (Sjöqvist et al., 2015).

Speciation usually involves the accumulation of multiple reproductive barriers that interact with each other during the process of divergence (Smadja & Butlin, 2011). Thus, in order to fully understand the causes of reproductive isolation, future studies must try to identify all contributing barriers. The extensive variation in life-history traits (including sex determination) among marine species offers unique opportunities to test hypotheses about the relative contributions of various reproductive barriers to speciation in different marine organisms and ecosystems. However, despite some progress, also illustrated in this special issue, we still have a long way to go.

2.3 | Characterising the genomic architecture of reproductive isolation

Understanding the genomic architecture of speciation—that is the number, relative effect sizes and genomic distribution of loci that underlie reproductive barriers—is currently one of the main endeavours of speciation research (Ravinet et al., 2017). Methodologies for studying genomic architecture have traditionally been classified as either being ‘top-down’—that is, those that attempt to identify loci underlying putative barrier traits—or being ‘bottom-up’—that is, those that attempt to identify signatures of selection in the genome without prior knowledge about isolating traits (Barrett & Hoekstra, 2011). Rather than taking one of these approaches, we encourage studies that use a combination of top-down and bottom-up approaches.

The most common approach to understanding the genomic architecture of isolating traits is quantitative trait locus (QTL) mapping (Moyle & Payseur, 2009). Facilitated by easy-to-use software (e.g. Broman et al., 2003) and new methods for marker discovery and genetic map construction (e.g. RADseq, Baird et al., 2008; Rastas, 2017), QTL mapping has now been applied to a wide variety of isolating traits, including prezygotic, extrinsic and intrinsic post-zygotic barriers (Berdan et al., 2021; Moyle & Payseur, 2009). The biggest technical challenge for most systems is the need to produce and rear large mapping families in the laboratory, an issue that is especially pertinent to the study of marine organisms, as previously mentioned. When this cannot be done, genome-wide association studies (GWAS) may provide an alternative means for inferring the architecture of isolating traits from natural populations (Kess et al., 2021). However, GWAS methods usually require a high-quality

reference genome, resequencing data for many individuals and are based on assumptions that are unlikely to hold in many cases of speciation, such as absence of population structure and high levels of historical recombination. These limitations can be partly circumvented by methods that take ancestry in interbreeding populations into account (so-called admixture mapping; Buerkle & Lexer, 2008).

Working from the bottom-up, genome scans have now become a widely used tool for identifying putative barrier loci based on molecular signatures of selection (Ravinet et al., 2017). These methods involve measuring genetic divergence (e.g. F_{ST} or d_{xy}) or admixture proportions (Martin et al., 2015) for thousands to millions of loci in order to identify sites in the genome where variation is inconsistent with a model of neutral divergence. Although the interpretation of patterns of genome-wide variation is not as straightforward as once thought (Ravinet et al., 2017), regions of the genome exhibiting exceptional divergence may be considered candidate barrier loci. Inferences from genome scans are strongest when they are based on whole-genome sequences rather than reduced-representation sequencing methods (e.g. RADseq), and when potentially confounding factors are also taken into account (Ravinet et al., 2017; see Ravinet et al., this issue, for an example).

These two approaches have also proven useful in revealing how structural genomic variation has contributed to the architecture of speciation. Given that strong reproductive isolation is usually caused by genetic differences at many loci, any mechanism or genomic feature that strengthens barriers is likely to favour local adaptation and speciation (Butlin & Smadja, 2018; Yeaman & Whitlock, 2011). Chromosomal rearrangements, especially inversions, are thought to play an important role in speciation by drastically reducing recombination across potentially large regions of the genome in interspecific hybrids with alternative arrangements (Faria & Navarro, 2010; Kirkpatrick & Barton, 2006). If inversions trap or accumulate multiple barrier loci, this can strengthen the integrity of reproductive barriers through the maintenance of linkage disequilibrium in the presence of gene flow (i.e. coupling). Given the relatively high dispersal of many marine species, it can be hypothesized that chromosomal rearrangements (and regions of low recombination in general) could play a particularly important role in facilitating speciation in marine ecosystems, mainly across steep environmental gradients. However, evaluating the relative importance of chromosomal rearrangements, namely inversions, in adaptation and speciation, is not always straightforward. Linkage disequilibrium within inverted regions can result in high differentiation across large genomic distances, even if they only contain a single locus involved in adaptation and reproductive isolation (Westram et al., 2020). This can make it seem like inversions contribute more to adaptation and speciation than they really do.

New approaches for identifying structural variation suggest that inversions are not uncommon among marine species (Johannesson et al., 2020; Mérot et al., 2020). Data recently gathered from some marine fish species support that inversions might play a central role in local adaptation, population divergence and potentially also speciation (Barth et al., 2019; Cayuela et al., 2020; Han et al., 2020; Le Moan et al., 2020). Notably, several large

putative inversions recently detected in the marine snail *Littorina saxatilis* (Faria et al., 2019) are enriched for loci involved in divergence between ecotypes across the species' distribution (Kess et al., 2021; Morales et al., 2019; Westram et al., 2018). Something similar could shape ecotype divergence in the related species *L. fabalis* (Galindo et al., 2021; Tatarenkov & Johannesson, 1999). The contribution of Berdan et al. (2021) highlights another interesting example, where a chromosomal fusion was found to harbour both loci involved in sex determination and intrinsic incompatibility, in line with the expectations of Haldane's rule. Despite these advances, the study of the role of chromosomal rearrangements in the diversification of marine life is still in its infancy. In a recent review, only 2 of 23 species showing inversions recently studied using genomic tools were marine (Wellenreuther & Bernatchez, 2018). More work is needed to establish a clear link between chromosomal rearrangements and reproductive isolation to evaluate their general importance in marine speciation.

2.4 | Inferring the history of divergence and speciation

One of the most challenging areas of speciation research, not limited to marine systems, is concerned with understanding the historical demographic events that accompany the evolution of reproductive isolation. This problem has a long history centred mainly around debates about the relative importance of different geographic modes of speciation in generating the current diversity and distribution of organisms (i.e. allopatric, parapatric and sympatric speciation). However, this traditional classification of speciation in terms of geographic context of divergence has more recently fallen out of favour (Butlin et al., 2008). Speciation can involve changes in the size of populations (i.e. population expansions and contractions) and episodes of isolation alternated by periods of gene flow associated with major environmental, geological and oceanographic changes (e.g. glaciations; see Laakkonen et al., 2021). Although clues about the demographic history of speciation can be inferred from geological evidence or climate modelling, it is often unclear whether divergence occurred with continuous gene flow or during a period of geographic isolation subsequently maintained by barriers to gene flow upon secondary contact. The main problem for speciation researchers is that these alternative histories can have very similar genetic signatures, so they are extremely difficult to tell apart (figure 3 in Ravinet et al., 2017). The recent access to large genomic data sets, which are information-rich and can be analysed using model-based inference tools, has proven very valuable in helping to distinguish alternative demographic scenarios also in marine taxa (e.g. Duranton et al., 2018; Le Moan et al., 2020; Momigliano et al., 2017; Popovic et al., 2021; Stankowski et al., 2020).

In this issue, Leder et al. (2021) used such a data set to infer the historical demography associated with speciation in sand gobies that inhabit a steep salinity gradient between the Baltic Sea and the

North Sea. Many of the successful colonizers of the Baltic Sea show evidence of adaptation to lower salinity and reproductive isolation from North Sea populations (Johannesson et al., 2020). However, it is sometimes not clear whether the divergence of brackish populations occurred with continuous gene flow along the gradient, or whether local adaptation was facilitated by a period of geographic isolation between high and low salinity populations. Using demographic modelling, the authors suggest that divergence between low- and high-salinity populations (~200,000 years ago) predates the formation of the Baltic Sea (8,000–10,000 years ago), although the period of secondary contact, when the current barriers probably emerged, roughly corresponds to the last glacial retreat.

In another contribution to this volume, Prada and Hellberg (2021) revisited the history of divergence between two ecotypes of the Caribbean candelabrum coral associated with a steep environmental gradient in water depth. Analysing an unprecedented number of markers for this system with demographic modelling tools, the authors aimed to distinguish between primary divergence and secondary contact between the two ecotypes. However, they show that the divergence scenario may have been more complex, with an initial period (~800,000 years ago) of asymmetric gene flow followed by a phase of complete isolation, and a more recent period where gene flow was re-established symmetrically at lower levels. Interestingly, this sequence of events is similar to that found in two other coral species whose divergence is also related to a depth gradient, making the authors ask whether an intermediate period of isolation is critical for speciation in these and other corals.

As Leder et al. (2021) point out, distinguishing alternative demographic histories is difficult even with modern genomic data sets, so individual studies should be interpreted with some caution (see also Momigliano et al., 2020). However, by applying a similar approach to many marine organisms inhabiting a broad range of environments, we may eventually be able to address more general questions about the history of speciation in our oceans. Is geographic isolation less important in marine compared with terrestrial organisms? Does the demography of speciation vary strongly between marine biomes, including coastal versus benthic environments and the open ocean? Finally, does the greater dispersal propensity of some marine organisms prevent allopatric speciation altogether?

2.5 | Studying hybridization and introgression

We also encourage more in-depth studies of hybridization and introgression encompassing a diverse array of marine organisms and environments. In general, it is difficult to overstate the contribution that hybrid zones have made to our general understanding of the speciation process. Unlike experimental crosses in the laboratory, hybrid zones allow us to understand how barriers to gene flow play out in the real world over time scales that are more relevant to the long-term persistence of species boundaries. Coupled with a rich body of theoretical work and powerful methods (Barton & Gale, 1993; Barton & Hewitt, 1985), it is not surprising that hybrid

zones have been described as 'natural laboratories' and 'windows' of the evolutionary process (Harrison, 1990; Hewitt, 1988).

Although some highly detailed studies of marine hybrid zones have been conducted (e.g. Westram et al., 2018), the vast majority have focused on terrestrial environments. For example, in a recent meta-analysis of hybrid zones by McEntee et al. (2020), only 6 of 131 (4.58%) were conducted on marine systems. This strong bias towards terrestrial studies is unlikely to be due to a lower incidence of hybridization in marine organisms, which is now thought to be relatively common (Gardner, 1997; Johannesson et al., 2020). Instead, it is more likely to reflect the general challenges mentioned above that come with working in many marine environments. For example, some hybrid zones are known to occur along light and depth gradients rather than across two-dimensional space (Hudson et al., 2020; Prada & Hellberg, 2021), making them difficult to discover and sample. A higher abundance of cryptic species could also reduce our capacity to identify marine hybrid zones (Gardner, 1997). Finally, because patterns of dispersal in marine organisms can be long range and strongly impacted by currents, patterns of hybridization can sometimes be spatially complex, making the geographic characterization and analysis of marine hybrid zones more difficult.

The geographic complexity of marine hybrid zones is highlighted by a paper in this issue that elucidates patterns of hybridization and introgression in a species complex of marine mussels (Simon et al., 2021). Overall, complex spatial patterns of hybridization and introgression between different *Mytilus* taxa have been shaped by both contemporary and historical contacts during the Quaternary period, including asymmetrical introgression at specific loci in populations closer to hybrid zones than further apart. Importantly, this study highlights the utility of studying genome-wide patterns of hybridization across populations at different distances from the contact zone to inform us about adaptive introgression and on how reproductive barriers decay (Ravinet et al., 2021; Simon et al., 2021).

The repeatability of differentiation among multiple introduced populations can also be informative about genomic signatures of reproductive barriers. In this volume, Popovic et al. (2021) used transcriptome markers to characterize multiple introductions of *Mytilus galloprovincialis* across the world. Their results showed that pre-introduction introgression with *M. edulis* in its native range was important for shaping the genomic patterns of hybridization patterns between introduced and native species. This adds to the evidence for an influence of ancient introgression in shaping the current genomic architecture of reproductive isolation between marine species (Duranton et al., 2018; Simon et al., 2021).

Another manuscript in this issue characterizes genome-wide patterns of introgression to understand how variation in the degree of habitat isolation shapes barriers to gene flow between anadromous Japan Sea stickleback (*G. nipponicus*) and the Pacific Ocean three-spined stickleback (*G. aculeatus*; Ravinet et al., 2021). Using a combination of ABBA-BABA statistics and window-based topology weighting to analyse whole-genome sequence data (among other approaches), the authors show that the overall levels of introgression were higher in a pair of populations with overlapping breeding

habitats than in a pair with separated spawning sites. Although this pattern suggests that isolation between breeding habitats contributes to reproductive isolation in this system, Ravinet et al. (2021) concluded that other reproductive barriers, including post-zygotic isolation, must be important in keeping the species distinct.

The comparison of hybridization rates between allopatric and sympatric species pairs offers a generally useful strategy to test for reinforcement in marine systems (e.g. Hollander et al., 2018). In this special issue, Tatarenkov et al.'s (2021) study of hermaphroditic *Rivulus* mangrove killifish that reproduce mainly by self-fertilization revealed higher hybridization and introgression between sympatric than allopatric populations of divergent lineages, a pattern that is opposite to that predicted by reinforcement. In contrast, the contribution by Berdan et al. (2021) suggests that reinforcement could have occurred during the divergence of *Lucania* killifish species associated with a salinity gradient. Clearly, more such studies are needed before strong conclusions about the contributions of reinforcement in marine speciation can be drawn. The study by Tatarenkov et al. (2021) also suggests that self-fertilization does not completely prevent gene flow between mangrove *Rivulus* killifish lineages and that hybridization can be important to avoid inbreeding depression and the extinction of different lineages. The study of how warming conditions can influence hybridization and species ranges is also important to predict how anthropogenic changes may influence speciation patterns in marine environments (Hudson et al., 2021).

Finally, another interesting outcome of hybridization is the formation of new hybrid species (i.e. hybrid speciation: Abbott et al., 2013). Hybrid speciation has been suggested for a variety of marine organisms, including fishes, molluscs, algae and even mammals (Amaral et al., 2014; Bringloe et al., 2020 and refs. therein; Väinölä & Johannesson, 2017; but see Schumer et al., 2014). However, information is yet too scarce to understand its relative frequency and importance in marine environments.

All these different investigations highlight how detailed studies of hybridization and introgression can enhance our understanding of many processes that are relevant to speciation. However, as previously mentioned, intertidal and estuarine habitats are easier to access than other marine environments such as the deep sea and open ocean. Despite this, there are a few pioneering studies that have explored the geographic and genomic complexity of organisms in these challenging environments (Choo et al., 2021; Faure et al., 2009; Kashtan et al., 2014). More studies of hybridization and hybrid zones are clearly needed.

2.6 | Implementing highly collaborative, interdisciplinary research

One of the main roadblocks to our understanding is that the study of speciation requires integration of detailed information from multiple sources. For example, although they have become a major focus of speciation studies, genomic data alone are unlikely to be sufficient to identify the main reproductive barriers between

closely related species (Ravinet et al., 2017). Studies targeting traits and environmental parameters that are candidates to be involved in speciation are also necessary to establish links between genotypes, phenotypes and environments during the evolution of reproductive isolation.

Progress towards understanding the mechanisms of speciation in marine organisms will likely benefit from collaborations of multiple researchers from different areas of expertise, as well as from improved integration of knowledge from multiple sources ranging from marine ecology to engineering. Although crucial also in other environments, the technological component may be greater in marine ecosystems, mainly for targeting less accessible habitats. Geological and paleontological studies are also essential for understanding the evolutionary history of species including the dating of divergence times (e.g. the Messenian crisis in the Mediterranean Sea; Hodge & Bellwood, 2016; Knowlton et al., 1993), as well as to inform about historical connectivity and gene flow between basins that are no longer interconnected. The study of post-glacial formations of new marine environments due to sea level rises offers interesting opportunities to study overlapping hybrid zones of multiple species and the importance of in situ divergence and reinforcement of older barriers formed during periods of isolation (Johannesson et al., 2020). Combining empirical data with modelling or theoretical approaches further aids in contrasting various evolutionary hypotheses under a proper statistical framework (Westram et al., 2018).

The potential for the spread of seeds or larvae can be modelled by combining species biology and oceanographic information into biophysical models (Jahnke et al., 2018). Structural biology, as exemplified by the classical studies of sea urchin and abalone egg-sperm incompatibilities, is also highly important for the study of reproductive barriers in broadcast spawning taxa, so more studies of gametic interactions are warranted (Palumbi, 2008). Functional and physiological studies are also crucial to understand the link between genotype and phenotype during local adaptation and speciation (e.g. Colosimo et al., 2005). Recent tools (e.g. CRISPR-Cas9) are now starting to be applied in some marine organisms (Momose & Concordet, 2016), offering promising new methods to experimentally investigate genes that have been identified as candidates playing a role in reproductive isolation using other approaches.

Some species of microalgae and bacteria have dormant stages that can be revived from dated sediment layers. These can be used as historical archives spanning several thousands of generations back in time, offering unique possibilities to detect evolutionary changes in both phenotype and genotype (e.g. Härnström et al., 2011). The study of ancient DNA in marine organisms also opens the possibility for directly assessing range shifts related to major geological or climatic events, to identify demographic changes and to validate the history of divergence inferred from modern samples (e.g. Rey-Iglesia et al., 2020), including the question of whether gene flow has been decreasing during divergence.

Fostered by climate change research, environmental data for multiple parameters that can influence speciation are increasingly

available worldwide (e.g. temperature). High-resolution characterization of the local environment using multiple tools for environmental monitoring (Bates et al., 2018) and niche modelling are essential for understanding the impact of ecology and natural selection on speciation in diverse marine environments. Studies establishing a connection between global and local environmental or ecological changes (Helmuth et al., 2014) are further needed to fully understand how global patterns influence speciation in specific marine biogeographic regions and local ecosystems.

3 | CONCLUDING REMARKS AND CONSERVATION IMPLICATIONS

In this special issue, we assembled several contributions to help highlight the need to learn more about speciation in marine environments. Although we acknowledge that many of the examples reflect our own (taxonomic, geographic, etc.) biases, we hope to inspire future research efforts in this topic to continue filling this critical gap.

The research on marine speciation highlighted here allows us to draw some preliminary conclusions. First, the term marine speciation encapsulates a huge diversity of life-history traits and reproductive barriers across multiple marine taxonomic groups and ecosystems. Thus, except for the sake of convenience, the classification of speciation as being marine, terrestrial and freshwater is probably not so useful to move the field forward. This, however, does not exclude the possibility of some reproductive barriers being more common in marine organisms or ecosystems. Second, in agreement with the relatively high dispersal of many marine species and the frequent lack of clear geographic barriers, gene flow seems common during speciation. Third, the large effective population size of many marine species probably entails increased levels of standing genetic variation upon which selection can act. Together with the role of ecology in driving marine species divergence, this suggests that natural selection may be particularly important in driving speciation at least in some marine taxa and ecosystems. Fourth, studies showing that particular genomic architectures (e.g. chromosomal rearrangements) prevent recombination between allelic variants underlying various reproductive barriers are relatively common in marine species. The large effective population sizes and connectivity observed in many marine species can maintain polymorphic rearrangements for long periods of time, which may at some point become instrumental in speciation (Wellenreuther & Bernatchez, 2018). Nevertheless, none of these conclusions are exclusive to marine ecosystems. Thus, more work is needed to determine what, if anything, makes speciation in marine environments different from terrestrial or freshwater ecosystems.

The patterns of biodiversity observed in our oceans reflect a balance between speciation and extinction. It is important to emphasize that anthropogenic threats to marine life (overfishing and hunting, acidification, warming, habitat fragmentation, the introduction of invasive species, pollution, etc.) do not only affect

extinction of marine populations and species, but also can have important consequences for the rates and dynamics of speciation in marine environments as well (e.g. Viard et al., 2020). Now that we are entering the United Nations decade of ocean science for sustainable development (2021–2030), there is urgent need for understanding how anthropogenic disturbances (global warming, ocean acidification, etc.) influence not only population and species survival (Fuller et al., 2020), but also the outcomes of hybridization (Hudson et al., 2021) and, ultimately, speciation rates. Enhanced knowledge of marine speciation will therefore improve marine biodiversity forecasting and lead to more informed conservation measures for many marine organisms.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

All authors contributed for designing the structure and writing the manuscript.

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REFERENCES

- Abbott, R., Albach, D., Ansell, S., Arntzen, J. W., Baird, S. J. E., Bierne, N., Boughman, J., Brelsford, A., Buerkle, C. A., Buggs, R., Butlin, R. K., Dieckmann, U., Eroukhanoff, F., Grill, A., Cahan, S. H., Hermansen, J. S., Hewitt, G., Hudson, A. G., Jiggins, C., ... Zinner, D. (2013). Hybridization and speciation. *Journal of Evolutionary Biology*, 26(2), 229–246. <https://doi.org/10.1111/j.1420-9101.2012.02599.x>
- Amaral, A. R., Lovell, G., Coelho, M. M., Amato, G., & Rosenbaum, H. C. (2014). Hybrid speciation in a marine mammal: The Clymene Dolphin (*Stenella clymene*). *PLoS One*, 9(1), e83645. <https://doi.org/10.1371/journal.pone.0083645>
- Andrén, T., Björck, S., Andrén, E., Conley, D., Zillén, L., & Anjar, J. (2011). The development of the Baltic Sea basin during the last 130 ka. In J. Harff, S. Björck, & P. Hoth (Eds.), *The Baltic Sea basin. Central and eastern European development studies (CEEDES)* (pp. 75–97). Springer Berlin.
- Baird, N. A., Etter, P. D., Atwood, T. S., Currey, M. C., Shiver, A. L., Lewis, Z. A., Selker, E. U., Cresko, W. A., & Johnson, E. A. (2008). Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS One*, 3, e3376. <https://doi.org/10.1371/journal.pone.0003376>
- Barrett, R. D. H., & Hoekstra, H. E. (2011). Molecular spandrels: Tests of adaptation at the genetic level. *Nature Reviews Genetics*, 12, 767–780. <https://doi.org/10.1038/nrg3015>
- Barrio, A. M., Lamichhane, S., Fan, G., Rafati, N., Pettersson, M., Zhang, H., Dainat, J., Ekman, D., Höppner, M., Jern, P., Martin, M., Nystedt, B., Liu, X., Chen, W., Liang, X., Shi, C., Fu, Y., Ma, K., Zhan, X., ... Andersson, L. (2016). The genetic basis for ecological adaptation of the Atlantic herring revealed by genome sequencing. *eLife*, 5, e12081.
- Barth, J. M. I., Villegas-Ríos, D., Freitas, C., Moland, E., Star, B., André, C., ... Jentoft, S. (2019). Disentangling structural genomic and behavioral barriers in a sea of connectivity. *Molecular Ecology*, 28, 1394–1411.
- Barton, N. H., & Gale, K. S. (1993). Genetic analysis of hybrid zones. In R. G. Harrison (Ed.), *Hybrid zones and the evolutionary process* (pp. 13–45). Oxford University Press.
- Barton, N. H., & Hewitt, G. M. (1985). Analysis of hybrid zones. *Annual Review of Ecology and Systematics*, 16(1), 113–148. <https://doi.org/10.1146/annurev.es.16.110185.000553>
- Bates, A. E., Helmuth, B., Burrows, M. T., Duncan, M. I., Garrabou, J., Guy-Haim, T., Lima, F., Queiros, A. M., Seabra, R., Marsh, R., Belmaker, J., Bensoussan, N., Dong, Y., Mazaris, A. D., Smale, D., Wahl, M., & Rilov, G. (2018). Biologists ignore ocean weather at their peril. *Nature*, 560, 299–301. <https://doi.org/10.1038/d41586-018-05869-5>
- Berdan, E. L., Fuller, R. C., & Kozak, G. M. (2021). Genomic landscape of reproductive isolation in *Lucania killifish*: The role of sex loci and salinity. *Journal of Evolutionary Biology*, 34, 157–174. <https://doi.org/10.1111/jeb.13725>
- Bierne, N., Bonhomme, F., & Arnaud-Haond, S. (2016). Dedicated population genomics for the silent world: The specific questions of marine population genetics. *Current Zoology*, 62, 545–550.
- Bierne, N., Bonhomme, F., & David, P. (2003). Habitat preference and the marine-speciation paradox. *Proceedings of the Royal Society B: Biological Sciences*, 270, 1399–1406. <https://doi.org/10.1098/rspb.2003.2404>
- Bierne, N., Welch, J., Loire, E., Bonhomme, F., & David, P. (2011). The coupling hypothesis: Why genome scans may fail to map local adaptation genes. *Molecular Ecology*, 20, 2044–2072. <https://doi.org/10.1111/j.1365-294X.2011.05080.x>
- Bringloe, T. T., Starko, S., Wade, R. M., Vieira, C., Kawai, H., De Clerck, O., Cock, J. M., Coelho, S. M., Destombe, C., Valero, M., Neiva, J., Pearson, G. A., Faugeton, S., Serrão, E. A., & Verbruggen, H. (2020). Phylogeny and evolution of the brown algae. *Critical Reviews in Plant Sciences*, 39, 281–321. <https://doi.org/10.1080/07352689.2020.1787679>
- Broman, K. W., Wu, H., Sen, S., & Churchill, G. A. (2003). R/qtl: QTL mapping in experimental crosses. *Bioinformatics*, 19(7), 889–890. <https://doi.org/10.1093/bioinformatics/btg112>

- Buerkle, C. A., & Lexer, C. (2008). Admixture as the basis for genetic mapping. *Trends in Ecology and Evolution*, 23, 686–694. <https://doi.org/10.1016/j.tree.2008.07.008>
- Butlin, R. (1987). Speciation by reinforcement. *Trends in Ecology & Evolution*, 2, 8–13. [https://doi.org/10.1016/0169-5347\(87\)90193-5](https://doi.org/10.1016/0169-5347(87)90193-5)
- Butlin, R. K., Galindo, J., & Grahame, J. W. (2008). Sympatric, parapatric or allopatric: The most important way to classify speciation? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 2997–3007. <https://doi.org/10.1098/rstb.2008.0076>
- Butlin, R. K., & Smadja, C. M. (2018). Coupling, Reinforcement, and Speciation. *American Naturalist*, 191(2), 155–172.
- Cayuela, H., Rougemont, Q., Laporte, M., Mérot, C., Normandeau, E., Dorant, Y., Tørresen, O. K., Hoff, S. N. K., Jentoft, S., Sirois, P., Castonguay, M., Jansen, T., Praebel, K., Clément, M., & Bernatchez, L. (2020). Shared ancestral polymorphisms and chromosomal rearrangements as potential drivers of local adaptation in a marine fish. *Molecular Ecology*, 29, 2379–2398. <https://doi.org/10.1111/mec.15499>
- Choo, L. Q., Bal, T. M. P., Goetze, E., & Peijnenburg, K. T. C. A. (2021). Oceanic dispersal barriers in a holoplanktonic gastropod. *Journal of Evolutionary Biology*, 34, 224–240. <https://doi.org/10.1111/jeb.13735>
- Colosimo, P. F., Hosemann, K. E., Balabhadra, S., Villareal, G. Jr, Dickson, M., Grimwood, J., & Kingsley, D. M. (2005). Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. *Science*, 307, 1928–1933. <https://doi.org/10.1126/science.1107239>
- Costa, A. P. B., Fruet, P. F., Secchi, E. R., Daura-Jorge, F. G., Simões-Lopes, P. C., Di Tullio, J. C., & Rosel, P. E. (2021). Ecological divergence and speciation in common bottlenose dolphins in the western South Atlantic. *Journal of Evolutionary Biology*, 34, 16–32. <https://doi.org/10.1111/jeb.13575>
- Costa, C., Fanelli, E., Marini, S., Danovaro, R., & Aguzzi, J. (2020). Global deep-sea biodiversity research trends highlighted by science mapping approach. *Frontiers in Marine Science*, 7, 384. <https://doi.org/10.3389/fmars.2020.00384>
- Duranton, M., Allal, F., Fraïsse, C., Bierne, C., Bonhomme, F., & Gagnaire, P.-A. (2018). The origin and remolding of genomic islands of differentiation in the European sea bass. *Nature Communications*, 9, 2518. <https://doi.org/10.1038/s41467-018-04963-6>
- Duranton, M., Allal, F., Valière, F., Bouchez, O., Bonhomme, F., & Gagnaire, P.-A. (2020). The contribution of ancient admixture to reproductive isolation between European sea bass lineages. *Evolution Letters*, 4, 226–242. <https://doi.org/10.1002/evl3.169>
- Ellison, C. K., & Burton, R. S. (2008). Genotype-dependent variation of mitochondrial transcriptional profiles in interpopulation hybrids. *Proceedings of the National Academy of Sciences of the United States of America*, 105(41), 15831–15836. <https://doi.org/10.1073/pnas.0804253105>
- Faria, R., Chaube, P., Morales, H. E., Larsson, T., Lemmon, A. R., Lemmon, E. M., ... Butlin, R. K. (2019). Multiple chromosomal rearrangements in a hybrid zone between *Littorina saxatilis* ecotypes. *Molecular Ecology*, 28, 1375–1393.
- Faria, R., & Navarro, A. (2010). Chromosomal speciation revisited: Rearranging theory with pieces of evidence. *Trends in Ecology & Evolution*, 25, 660–669. <https://doi.org/10.1016/j.tree.2010.07.008>
- Faure, B., Jollivet, D., Tanguy, A., Bonhomme, F., & Bierne, N. (2009). Speciation in the deep sea: Multi-locus analysis of divergence and gene flow between two hybridizing species of hydrothermal vent mussels. *PLoS One*, 4(8), e6485. <https://doi.org/10.1371/journal.pone.0006485>
- Foote, A. D., Vijay, N., Ávila-Arcos, M. C., Baird, R. W., Durban, J. W., Fumagalli, M., Gibbs, R. A., Hanson, M. B., Korneliusen, T. S., Martin, M. D., Robertson, K. M., Sousa, V. C., Vieira, F. G., Vinař, T., Wade, P., Worley, K. C., Excoffier, L., Morin, P. A., Gilbert, M. T. P., & Wolf, J. B. W. (2016). Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nature Communications*, 7, 11693. <https://doi.org/10.1038/ncomms11693>
- Fuller, Z. L., Mocellin, V. J. L., Morris, L. A., Shepperd, J., Sarre, L., Peng, J., ... Przeworski, M. (2020). Population genetics of the coral *Acropora millepora*: Toward genomic prediction of bleaching. *Science*, 369, eaba4674.
- Galindo, J., Carvalho, J., Sotelo, G., Duveitop, M., Costa, D., Kempainen, P., & Faria, R. (2021). Genetic and morphological divergence between *Littorina fabalis* ecotypes in Northern Europe. *Journal of Evolutionary Biology*, 34, 97–113. <https://doi.org/10.1111/jeb.13705>
- Galtier, N. (2016). Adaptive protein evolution in animals and the effective population size hypothesis. *PLoS Genetics*, 12, e1005774. <https://doi.org/10.1371/journal.pgen.1005774>
- Gardner, J. P. A. (1997). Hybridization in the sea. *Advances in Marine Biology*, 31, 1–78.
- Han, F., Jamsandekarm, M., Pettersson, M. E., Su, L., Fuentes-Prado, A. P., Davids, B. W., ... Andersson, L. (2020). Ecological adaptation in Atlantic herring is associated with large shifts in allele frequencies at hundreds of loci. *eLife*, 9, e61076.
- Härnström, K., Ellegaard, M., Andersen, T. J., & Godhe, A. (2011). Hundred years of genetic structure in a sediment revived diatom population. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 4252–4257. <https://doi.org/10.1073/pnas.1013528108>
- Harrison, R. G. (1990). Hybrid zones: Windows on evolutionary process. *Oxford Surveys in Evolutionary Biology*, 7, 59.
- Helmuth, B., Russell, B. D., Connell, S. D., Dong, Y., Harley, C. D. G., Lima, F. P., Sará, G., Williams, G. A., & Mieszkowska, N. (2014). Beyond long-term averages: Making biological sense of a rapidly changing world. *Climate Change Responses*, 1, 6. <https://doi.org/10.1186/s40665-014-0006-0>
- Hewitt, G. M. (1988). Hybrid zones-natural laboratories for evolutionary studies. *Trends in Ecology & Evolution*, 3, 158–167. [https://doi.org/10.1016/0169-5347\(88\)90033-X](https://doi.org/10.1016/0169-5347(88)90033-X)
- Hodge, J. R., & Bellwood, D. R. (2016). The geography of speciation in coral reef fishes: The relative importance of biogeographical barriers in separating sister-species. *Journal of Biogeography*, 43, 1324–1335. <https://doi.org/10.1111/jbi.12729>
- Hollander, J., Montaña-Rendón, M., Bianco, G., Yang, X., Westram, A. M., Duvaux, L., ... Butlin, R. K. (2018). Are assortative mating and genital divergence driven by reinforcement? *Evolution Letters*, 2(6), 557–566.
- Holman, L. E., de Bruyn, M., Creer, S., Carvalho, G., Robidart, J., & Rius, M. (2019). Detection of introduced and resident marine species using environmental DNA metabarcoding of sediment and water. *Scientific Reports*, 9, 11559. <https://doi.org/10.1038/s41598-019-47899-7>
- Hudson, J., Johannesson, K., McQuaid, C. D., & Rius, M. (2020). Secondary contacts and genetic admixture shape colonisation by an amphiatlantic epibenthic invertebrate. *Evolutionary Applications*, 13, 600–612.
- Hudson, J., McQuaid, C. D., & Rius, M. (2021). Contemporary climate change hinders hybrid performance of ecologically dominant marine invertebrates. *Journal of Evolutionary Biology*, 34, 60–72. <https://doi.org/10.1111/jeb.13609>
- Jahnke, M., Jonsson, P. R., Moksnes, P.-O., Loo, L.-O., Jacobi, M. N., & Olsen, J. L. (2018). Seascape genetics and biophysical connectivity modelling support conservation of the seagrass *Zostera marina* in the Skagerrak-Kattegat region of the eastern North Sea. *Evolutionary Applications*, 11, 645–661.
- Jezkova, T., & Wiens, J. J. (2017). What explains patterns of diversification and richness among animal phyla? *American Naturalist*, 189(3), 201–212. <https://doi.org/10.1086/690194>
- Johannesson, K. (2009). Inverting the null-hypothesis of speciation: A marine snail perspective. *Evolutionary Ecology*, 23, 5–16. <https://doi.org/10.1007/s10682-007-9225-1>

- Johannesson, K. (2015). What can be learnt from a snail? *Evolutionary Applications*, 9, 153–165. <https://doi.org/10.1111/eva.12277>
- Johannesson, K., Le Moan, A., Perini, S., & André, C. (2020). A Darwinian laboratory of multiple contact zones. *Trends in Ecology & Evolution*, 35, 1021–1036. <https://doi.org/10.1016/j.tree.2020.07.015>
- Johannesson, K., Rolán-Alvarez, E., & Ekdahl, A. (1995). Incipient reproductive isolation between two sympatric morphs of the intertidal snail *Littorina saxatilis*. *Evolution*, 49, 1180–1190.
- Johannesson, K., Zagrodzka, Z., Faria, R., Westram, A. M., & Butlin, R. K. (2020). Is embryo abortion a postzygotic barrier to gene flow between *Littorina* ecotypes? *Journal of Evolutionary Biology*, 33, 342–351.
- Johnson, Z. I., Zinser, E. R., Coe, A., McNulty, N. P., Malcolm, E., Woodward, S., & Chisholm, S. W. (2006). Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients. *Science*, 311(5768), 1737–1740. <https://doi.org/10.1126/science.1118052>
- Jones, F. C., Grabherr, M. G., Chan, Y. F., Russell, P., Mauceli, E., Johnson, J., Swofford, R., Pirun, M., Zody, M. C., White, S., Birney, E., Searle, S., Schmutz, J., Grimwood, J., Dickson, M. C., Myers, R. M., Miller, C. T., Summers, B. R., Knecht, A. K., ... Kingsley, D. M. (2012). The genomic basis of adaptive evolution in threespine sticklebacks. *Nature*, 484, 55–61. <https://doi.org/10.1038/nature10944>
- Kashtan, N., Roggensack, S. E., Rodrigue, S., Thompson, J. W., Biller, S. J., Coe, A., Ding, H., Marttinen, P., Malmstrom, R. R., Stocker, R., Follows, M. J., Stepanauskas, R., & Chisholm, S. W. (2014). Single-cell genomics reveals hundreds of coexisting subpopulations in wild *Prochlorococcus*. *Science*, 344, 416–420. <https://doi.org/10.1126/science.1248575>
- Kess, T., Brachmann, M., & Boulding, E. (2021). Putative chromosomal rearrangements are associated primarily with ecotype divergence rather than geographic separation in an intertidal, poorly-dispersing snail. *Journal of Evolutionary Biology*, 34, 193–207. <https://doi.org/10.1111/jeb.13724>
- Kirkpatrick, M., & Barton, N. (2006). Chromosome inversions, local adaptation and speciation. *Genetics*, 173, 419–434. <https://doi.org/10.1534/genetics.105.047985>
- Knowlton, N., Weigt, L. A., Solórzano, L. A., Mills, D. K., & Bermingham, E. (1993). Divergence in proteins, mitochondrial DNA, and reproductive compatibility across the Isthmus of Panama. *Science*, 260, 1629–1632. <https://doi.org/10.1126/science.8503007>
- Laakkonen, H. M., Hardman, M., Strelkov, P., & Väinölä, R. (2021). Cycles of trans-Arctic dispersal and vicariance, and diversification of the amphiboreal marine fauna. *Journal of Evolutionary Biology*, 34, 73–96. <https://doi.org/10.1111/jeb.13674>
- Lackey, A. C. R., & Boughman, J. W. (2016). Evolution of reproductive isolation in stickleback fish. *Evolution*, 71, 357–372. <https://doi.org/10.1111/evo.13114>
- Le Moan, A., Bekkevold, D., & Hemmer-Hansen, J. (2020). Evolution at two time-frames: Ancient and common origin of two structural variants involved in local adaptation of the European plaice (*Pleuronectes platessa*). *Heredity*. <https://doi.org/10.1038/s41437-020-00389-3>
- Leder, E. H., André, C., Moan, A. L., Töpel, M., Blomberg, A., Havenhand, J. N., ... Svensson, O. (2021). Post-glacial establishment of locally adapted fish populations over a steep salinity gradient. *Journal of Evolutionary Biology*, 34, 138–156. <https://doi.org/10.1111/jeb.13668>
- Lessios, H. A. (2007). Reproductive isolation between species of sea urchins. *Bulletin of Marine Science*, 81(2), 191–208.
- Lourenço, J. M., Glémin, S., & Galtier, N. (2013). The rate of molecular adaptation in a changing environment. *Molecular Biology and Evolution*, 30, 1292–1301. <https://doi.org/10.1093/molbev/mst026>
- Martin, S. H., Davey, J. W., & Jiggins, C. D. (2015). Evaluating the use of ABBA-BABA statistics to locate introgressed loci. *Molecular Biology and Evolution*, 32, 244–257. <https://doi.org/10.1093/molbev/msu269>
- Mayr, E. (1954). Geographic speciation in tropical echinoids. *Evolution*, 8, 1–18. <https://doi.org/10.1111/j.1558-5646.1954.tb00104.x>
- Mayr, E. (2001). Wu's genic view of speciation. *Journal of Evolutionary Biology*, 14, 866–867. <https://doi.org/10.1046/j.1420-9101.2001.00336.x>
- McEntee, J. P., Burleigh, J. G., & Singhal, S. (2020). Dispersal predicts hybrid zone widths across animal diversity: Implications for species borders under incomplete reproductive isolation. *American Naturalist*, 196, 9–28. <https://doi.org/10.1086/709109>
- Mérot, C., Oomen, R., Tigano, A., & Wellenreuther, M. (2020). A roadmap for understanding the evolutionary significance of structural genomic variation. *Trends in Ecology and Evolution*, 35, 561–572. <https://doi.org/10.1016/j.tree.2020.03.002>
- Miglietta, M. P., Faucci, A., & Santini, F. (2011). Speciation in the sea: Overview of the symposium and discussion of future directions. *Integrative and Comparative Biology*, 51, 449–455. <https://doi.org/10.1093/icb/acr024>
- Momigliano, P., Florin, A.-B., & Merilä, J. (2020). Biases in demographic modeling affect our understanding of the process of speciation. *bioRxiv*, <https://doi.org/10.1101/2020.06.03.128298>
- Momigliano, P., Jokinen, H., Fraimout, A., Florin, A.-B., Norrköb, A., & Merilä, J. (2017). Extraordinarily rapid speciation in a marine fish. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 6074–6079. <https://doi.org/10.1073/pnas.1615109114>
- Momose, T., & Concordet, J.-P. (2016). Diving into marine genomics with CRISPR/Cas9 systems. *Marine Genomics*, 30, 55–56. <https://doi.org/10.1016/j.margen.2016.10.003>
- Monteiro, C. A., Paulino, C., Jacinto, R., Serrão, E. A., & Pearson, G. A. (2016). Temporal windows of reproductive opportunity reinforce species barriers in a marine broadcast spawning assemblage. *Scientific Reports*, 6, 29198. <https://doi.org/10.1038/srep29198>
- Morales, H. E., Faria, R., Johannesson, K., Larsson, T., Panova, M., Westram, A. M., & Butlin, R. K. (2019). Genomic architecture of parallel ecological divergence: Beyond a single environmental contrast. *Science Advances*, 5, eaav9963. <https://doi.org/10.1126/sciadv.aav9963>
- Moyle, L. C., & Payseur, B. A. (2009). Reproductive isolation grows on trees. *Trends in Ecology & Evolution*, 24, 591–598. <https://doi.org/10.1016/j.tree.2009.05.010>
- Olsen, J. L., Stam, W. T., Coyer, J. A., Reusch, T. B. H., Billingham, M., Bostrom, C., Calvert, E., Christie, H., Granger, S., Lumière, R. L., Milchakova, N., Oudot-le seq, M.-P., Procaccini, G., Sanjabi, B., Serrão, E., Veldsink, J., Widdicombe, S., & Wyllie-echeverria, S. (2004). North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. *Molecular Ecology*, 13, 1923–1941. <https://doi.org/10.1111/j.1365-294X.2004.02205.x>
- Palumbi, S. R. (1992). Marine speciation on a small planet. *Trends in Ecology and Evolution*, 7, 114–118. [https://doi.org/10.1016/0169-5347\(92\)90144-Z](https://doi.org/10.1016/0169-5347(92)90144-Z)
- Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics*, 25, 547–572. <https://doi.org/10.1146/annurev.es.25.110194.002555>
- Palumbi, S. R. (2008). Speciation and the evolution of gamete recognition genes: Pattern and process. *Heredity*, 102, 66–76. <https://doi.org/10.1038/hdy.2008.104>
- Pereyra, R. T., Huenchunir, C., Johansson, D., Forslund, H., Kautsky, L., Jonsson, P. R., & Johannesson, K. (2013). Parallel speciation or long-distance dispersal? Lessons from seaweeds (*Fucus*) in the Baltic Sea. *Journal of Evolutionary Biology*, 26, 1727–1737.

- Perini, S., Rafajlovic, M., Johannesson, K., Westram, A. M., & Butlin, R. K. (2020). Assortative mating, sexual selection and their consequences for gene flow in *Littorina*. *Evolution*, *74*, 1482–1497.
- Popovic, I., Bierne, N., Gaiti, F., Tanurdžić, M., & Riginos, C. (2021). Pre-introduction introgression contributes to parallel differentiation and contrasting hybridisation outcomes between invasive and native marine mussels. *Journal of Evolutionary Biology*, *34*, 175–192. <https://doi.org/10.1111/jeb.13746>
- Potkamp, G., & Fransen, C. H. J. M. (2019). Speciation with gene flow in marine systems. *Contributions to Zoology*, *88*, 133–172. <https://doi.org/10.1163/18759866-20191344>
- Prada, C., & Hellberg, M. E. (2013). Long prereproductive selection and divergence by depth in a Caribbean candelabrum coral. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 3961–3966. <https://doi.org/10.1073/pnas.1208931110>
- Prada, C., & Hellberg, M. (2021). Speciation-by-depth on coral reefs: Sympatric divergence with gene flow or cryptic transient isolation? *Journal of Evolutionary Biology*, *34*, 128–137. <https://doi.org/10.1111/jeb.13731>
- Puebla, O. (2009). Ecological speciation in marine v. freshwater fishes. *Journal of Fish Biology*, *75*, 960–996.
- Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T. J., Coll, M., & Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, *559*, 392–395. <https://doi.org/10.1038/s41586-018-0273-1>
- Rastas, P. (2017). Lep-MAP3: Robust linkage mapping even for low-coverage whole genome sequencing data. *Bioinformatics*, *33*(23), 3726–3732. <https://doi.org/10.1093/bioinformatics/btx494>
- Ravinet, M., Faria, R., Butlin, R. K., Galindo, J., Bierne, N., Rafajlović, M., Noor, M. A. F., Mehlig, B., & Westram, A. M. (2017). Interpreting the genomic landscape of speciation: A road map for finding barriers to gene flow. *Journal of Evolutionary Biology*, *30*, 1450–1477. <https://doi.org/10.1111/jeb.13047>
- Ravinet, M., Kume, M., Ishikawa, A., & Kitano, J. (2021). Patterns of genomic divergence and introgression between Japanese stickleback species with overlapping breeding habitats. *Journal of Evolutionary Biology*, *34*, 114–127. <https://doi.org/10.1111/jeb.13664>
- Rey-Iglesia, A., Gaubert, P., Espregueira Themudo, G., Pires, R., De La Fuente, C., Freitas, L., Aguilar, A., Borrell, A., Krakhmalnaya, E., Vasconcelos, R., & Campos, P. F. (2020). Mitogenomics of the endangered Mediterranean monk seal (*Monachus monachus*) reveals dramatic loss of diversity and supports historical gene-flow between Atlantic and eastern Mediterranean populations. *Zoological Journal of the Linnean Society*, *zlaa084*. <https://doi.org/10.1093/zoolinnean/zlaa084>
- Ribardière, A., Pabion, E., Coudret, J., Daguin-Thiébaud, C., Houbin, C., Loisel, S., ... Broquet, T. (2021). Sexual isolation with and without ecological isolation in marine isopods *Jaera albifrons* and *J. praeheirsuta*. *Journal of Evolutionary Biology*, *34*, 33–48. <https://doi.org/10.1111/jeb.13559>
- Rocha, L. A., & Bowen, B. W. (2008). Speciation in coral-reef fishes. *Journal of Fish Biology*, *72*, 1101–1121. <https://doi.org/10.1111/j.1095-8649.2007.01770.x>
- Schumer, M., Rosenthal, G. G., & Andolfatto, P. (2014). How common is homoploid hybrid speciation? *Evolution*, *68*, 1553–1560. <https://doi.org/10.1111/evo.12399>
- Simon, A., Fraïsse, C., El Ayari, T., Liautard-Haag, C., Strelkov, P., Welch, J. J., & Bierne, N. (2021). How do species barriers decay? Concordance and local introgression in mosaic hybrid zones of mussels. *Journal of Evolutionary Biology*, *34*, 208–223. <https://doi.org/10.1111/jeb.13709>
- Sjöqvist, C., Godhe, A., Jonsson, P. R., Sundqvist, L., & Kremp, A. (2015). Local adaptation and oceanographic connectivity patterns explain genetic differentiation of a marine diatom across the North Sea-Baltic Sea salinity gradient. *Molecular Ecology*, *24*, 2871–2885. <https://doi.org/10.1111/mec.13208>
- Smadja, C. M., & Butlin, R. K. (2011). A framework for comparing processes of speciation in the presence of gene flow. *Molecular Ecology*, *20*, 5123–5140. <https://doi.org/10.1111/j.1365-294X.2011.05350.x>
- Stankowski, S., Westram, A. M., Zagrodzka, Z. B., Eyres, I., Broquet, T., Johannesson, K., & Butlin, R. K. (2020). The evolution of strong reproductive isolation between sympatric intertidal snails. *Proceedings of the Royal Society B: Biological Sciences*, *375*, 20190545.
- Swanson, W. J., & Vacquier, V. D. (1998). Concerted evolution in an egg receptor for a rapidly evolving abalone sperm protein. *Science*, *281*, 710–712. <https://doi.org/10.1126/science.281.5377.710>
- Tatarenkov, A., Earley, R. L., Taylor, D. S., Davis, W. P., & Avise, J. C. (2021). Extensive hybridization and past introgression between divergent lineages in a quasi-clonal hermaphroditic fish: Ramifications for species concepts and taxonomy. *Journal of Evolutionary Biology*, *34*, 49–59. <https://doi.org/10.1111/jeb.13624>
- Tatarenkov, A., & Johannesson, K. (1999). Micro- and macrogeographic allozyme variation in *Littorina fabalis*: do sheltered and exposed forms hybridize? *Biological Journal of the Linnean Society*, *67*, 199–212. <https://doi.org/10.1111/j.1095-8312.1999.tb01861.x>
- Väinölä, R., & Johannesson, K. (2017). Genetic diversity and evolution. In P. Leijonmalm-Snoeijs, H. Schubert, & T. Radziejewska (Eds.), *Biological oceanography of the Baltic sea* (pp. 223–253). Springer.
- van der Ven, R. M., Flot, J.-F., Buitrago-López, C., & Kochzius, M. (2020). Population genetics of the brooding coral *Seriatopora hystrix* reveals patterns of strong genetic differentiation in the Western Indian Ocean. *Heredity*. <https://doi.org/10.1038/s41437-020-00379-5>
- Viard, F., Rignios, C., & Bierne, N. (2020). Anthropogenic hybridization at sea: Three evolutionary questions relevant to invasive species management. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*, 20190547.
- Wellenreuther, M., & Bernatchez, L. (2018). Eco-evolutionary genomics of chromosomal inversions. *Trends in Ecology & Evolution*, *33*, 427–440. <https://doi.org/10.1016/j.tree.2018.04.002>
- Westram, A. M., Faria, R., Butlin, R., & Johannesson, K. (2020). Inversions and Evolution. In eLS. Chichester: John Wiley & Sons Ltd. <https://doi.org/10.1002/9780470015902.a0029007>
- Westram, A. M., Rafajlović, M., Chaube, P., Faria, R., Larsson, T., Panova, M., Ravinet, M., Blomberg, A., Mehlig, B., Johannesson, K., & Butlin, R. (2018). Clines on the seashore: The genomic architecture underlying rapid divergence in the face of gene flow. *Evolution Letters*, *2*, 297–309. <https://doi.org/10.1002/evl3.74>
- Yeaman, S., & Whitlock, M. C. (2011). The genetic architecture of adaptation under migration-selection balance. *Evolution*, *65*, 1897–1911. <https://doi.org/10.1111/j.1558-5646.2011.01269.x>

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