ICES Journal of Marine Science

ICES Journal of Marine Science (2018), doi:10.1093/icesjms/fsx244

Food for Thought

Integrating population genomics and biophysical models towards evolutionary-based fisheries management

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Baltazar-Soares, M., Hinrichsen, H.-H., and Eizaguirre C. Integrating population genomics and biophysical models towards evolutionary-based fisheries management. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsx244.

Received 11 July 2017; revised 8 December 2017; accepted 14 December 2017.

Overfishing and rapid environmental shifts pose severe challenges to the resilience and viability of marine fish populations. To develop and implement measures that enhance species' adaptive potential to cope with those pressures while, at the same time, ensuring sustainable exploitation rates is part of the central goal of fisheries management. Here, we argue that a combination of biophysical modelling and population genomic assessments offer ideal management tools to define stocks, their physical connectivity and ultimately, their short-term adaptive potential. To date, biophysical modelling has often been confined to fisheries ecology whereas evolutionary hypotheses remain rarely considered. When identified, connectivity patterns are seldom explored to understand the evolution and distribution of adaptive genetic variation, a proxy for species' evolutionary potential. Here, we describe a framework that expands on the conventional seascape genetics approach by using biophysical modelling and population genomics. The goals are to identify connectivity patterns and selective pressures, as well as putative adaptive variants directly responding to the selective pressures and, ultimately, link both to define testable hypotheses over species response to shifting ecological conditions and overexploitation.

Keywords: adaptive genetic variation, biophysical models, fisheries management, population genomics.

Introduction

The status of many oceanic fish populations is in a fragile state, bringing expected negative impacts on nature and society alike (Cardinale *et al.*, 2012; Worm and Branch, 2012). Not only ecosystem services provided by fisheries and fisheries-related activities directly affect the livelihood of ∼260 million people worldwide (Teh and Sumaila, 2013) but also the overexploitation of targeted species disrupts the balance and health of marine ecosystems at regional scales (Schindler *et al.*, 2010).

Fisheries management relies fundamentally on the definition of biological "stocks" (Ovenden *et al.*, 2015). These groups of individuals are considered population and management units and are expected to respond independently to various pressures. Thus, the exact definition of stocks' spatial–temporal boundaries, as well as the connectivity among stocks, are central to fisheries science (Ovenden *et al.*, 2015). While these research topics have been investigated for decades with a wide range of approaches, physical modelling of ocean environments (Andrello *et al.*, 2013; Teacher *et al.*, 2013), and genetic tools are becoming particularly informative (Hemmer-Hansen *et al.*, 2014b).

The concept of seascape genetics, which was introduced by Galindo *et al.* (2006), presents a unified framework to couple physical ocean modelling with genetic tools. Later on, Selkoe *et al.* (2008) suggested that seascape genetics could be used to investigate connectivity scenarios and hypotheses alternative to those obtained solely with genetic markers. Assuming passive larval dispersal, oceanographic currents provide more realistic models of dispersal and connectivity than those theoretically drawn from population genetics. By analysing genetic variation in a number of populations and simulating passive dispersal of individuals, it has been shown that oceanography can explain allele frequency shifts detected across fine geographic scales (Baltazar-Soares *et al.*, 2014; Schiavina *et al.*, 2014). The body of work that envelops seascape genetics primarily focuses on neutral evolving genetic markers, which does not allow investigating directly the adaptive genetic variation, a proxy for species' adaptive potential. Here, we define adaptive potential as a species'/population's ability to respond to selection by the means of phenotypic or molecular changes (Eizaguirre and Baltazar-Soares, 2014). For fisheries management, evaluating a species' adaptive potential is equivalent to estimating the resilience capacity of fish stocks to new and/or fluctuating selective pressures (Conover *et al.*, 2006; Marty *et al.*, 2015). The recent advances of genomics tools thus represent an opportunity to integrate the quantification of adaptive genetic variation in marine systems and to become a central component of the stakeholders' toolkit. Yet, a framework that summarizes both the use and the potential of those genomic advances to fisheries science, as well as a description of direct applications in fisheries management, is still lacking. It is obvious that the management of fisheries will also need to evolve with the technological advances occurring in many fields of research that constitute the core of such a multidisciplinary activity (Cooke *et al.*, 2014).

In this opinion piece, we suggest research directions that extend on the principles of seascape genetics towards the use of functional genetic variants—proxy for adaptability—while describing applications of potential findings to fisheries management. On the one hand, using biophysical modelling it is possible to include detailed biological information within hydrodynamic models (Miller, 2007; Hinrichsen *et al.*, 2011; Peck and Hufnagl, 2012; Hufnagl *et al.*, 2013). On the other hand, high throughput sequencing increases the power to detect highly differentiated genomic regions due to selection, with direct applications for monitoring (Allendorf *et al.*, 2010; Brodersen and Seehausen, 2014). We argue that such an approach will favour the study of evolutionary hypotheses underlying the distribution of adaptive genetic variation in marine fish species. This is because both fields are undergoing significant technological advances. In the one hand, increasing resolution of biophysical models facilitates the validation of physical and biological parameters, allowing for a more accurate hind- and forecasting ability and exploration of individual-based biological traits (Cury *et al.*, 2008; Metaxas and Saunders, 2009; Peck and Hufnagl, 2012). On the other hand, screens of genomes or transcriptomes as well as related analytical tools, enhance the statistical power to detect signatures of selection in an ever increasing number of non-model marine organisms (Ekblom and Galindo, 2011; Andrews *et al.*, 2016). The timing of an integrative framework specifically aimed at improving management comes from the fast-pace environmental changes affecting fish stocks, such as ocean warming (Hill *et al.*, 2016), ocean acidification (Munday *et al.*, 2010) or the expansion of oxygen minimum zones (Stramma *et al.*, 2008). This is particularly relevant in the case of exploited species, because fisheries impose an additional selective pressure that feeds back on adaptive traits (Ernande *et al.*, 2004; Kuparinen and Merila, 2007). The more we know about the evolution of traits and life history strategies, the more we will understand how fish will respond to novel and multi-fold environmental pressures.

This review is structured around four main axes: first, we will illustrate how natural processes govern population dynamics of marine fishes. Second, we will describe biophysical modelling and the different components that make it a suitable research tool in fisheries ecology. We will briefly introduce how well these models perform in identifying natural pressures acting upon a broad range of marine species (for detailed and specific reviews see, Miller, 2007; North *et al.*, 2009; Hinrichsen *et al.*, 2011; Peck and Hufnagl, 2012). Third, we will outline the recent advances in genome-wide screening techniques that facilitate the identification of candidate loci under selection in apparently genetically homogenous populations of marine fishes. Lastly, with key examples, we will illustrate how the outcomes of individual based-modelling and genomics can be integrated to explore hypothesis-driven evolutionary scenarios. Particularly, we will describe (i) how adaptive genetic variation can be inferred within structured populations after the identification of selective pressures through biophysical modelling; (ii) possible avenues of research to explore evolutionary history and adaptive potential of species where alternative life strategies were identified and validated through field observations and biophysical modelling. Lastly, we will elaborate on possible implications for management. We argue that such an exercise would provide important contributions to our understanding of the evolutionary ecology of marine fishes, and offer possibilities for fisheries management and conservation to implement the much warranted evolutionary-based perspective (Conover and Munch, 2002; Dunlop *et al.*, 2009). Our definition of "evolutionary-based management" is based on Conover and Munch (2002) and Dunlop *et al.* (2009), but follows the same philosophy as that of "evolutionary enlightened management" (Ashley *et al.*, 2003) and "evolutionarily informed management" (Smith *et al.*, 2014).

Impacts of ecological factors on the recruitment dynamics of marine fishes

Studies on how ecological factors impact the population dynamics of marine fishes date back to the beginning of the 20th century, e.g. (Hjort, 1914). These studies are primarily aimed at understanding how mortality of early life stages dictates recruitment and correlates with the abundance of adult fish (Houde, 2008). The high mortality experienced by early life stages probably relates to the evolution of broadcast spawning strategy—a common trait in marine fishes (Cowen *et al.*, 2000; Bode and Marshall, 2007). This *r*-strategy defines the release of an extremely high amount of gametes into the water column prior to fertilization (Adams, 1980). It is thought to have evolved as a bet-hedging adaptive response to variable environmental conditions (Bailey *et al.*, 2008). Some examples are those that link shifts in the abundance of fish or plankton to large scale hydro-climatic variations (Beaugrand, 2004). Horse-mackerel (*Trachurus trachurus*) in the North Sea (Reid *et al.*, 2001) or anchovies (*Engraulis ringens*) and sardines (*Sardina plichardus*) in the North East Pacific (Chavez *et al.*, 2003) see their abundances fluctuate alongside the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation (ENSO) respectively. However, their recruitment is probably regulated by fine scale mechanisms associated with variations of abiotic and biotic factors such as sea surface temperatures, hydrodynamic features, prey availability, and predation success (Cushing, 1974; Iles and Sinclair, 1982; Houde, 2008). As broadcast spawning fishes have evolved spawning time and location to target optimal environmental conditions (Colin, 1992;

Thorrold *et al.*, 2001; Bellier *et al.*, 2007), one cannot rule out the evolution of correlated traits in response to ecological pressures in the oceanic environment.

Biophysical modelling: concepts and applications in marine ecology

Biophysical modelling is currently used as an exploratory and complementary tool to traditional fisheries monitoring (North *et al.*, 2009). Conceptually, those models incorporate three elements: a hydrodynamic model that realistically simulates the physical oceanic environment, a particle tracking model that simulates the movement of virtual particles representing, for example, fish larvae, and a coupled model that mimics biological processes and/or behavioural activity (Peck and Hufnagl, 2012). These tools predict recruitment success and can be used to investigate connectivity (both among populations and among critical areas exploited by the same population), providing a better understanding of the factors mediating early life stage mortality (Peck and Hufnagl, 2012, Box 1 provides specific examples).

The hydrodynamic component forms the basis of biophysical models as it simulates the physical environment where interactions with biological processes occur (Hinrichsen, 2009). As hydrodynamic models *per se* are discrete equations that resolve velocities, turbulence, salinity, and temperature of a certain spatial–temporal scale, the incorporation of particle-tracking tools provides the empirical outcomes—in terms of movement—of those mathematical functions. This means that hydrodynamic models must be carefully validated before the implementation of particle-tracking tools (North *et al.*, 2009). Whereas general validations include correlations with known observational features, e.g. sea surface temperatures or salinity, more technical parameterization includes specified forcing, boundary conditions, initial conditions, and resolution of fine scale hydrodynamics (Fossette *et al.*, 2012). These validations are often associated with error quantification and sensitivity analyses and contribute to the resolution of hydrodynamic models (Gallego *et al.*, 2007; North *et al.*, 2009). Hydrodynamic models exist at many spatial and temporal resolutions and various extents. Examples of hydrodynamic models and how to choose them have been discussed elsewhere (Gibson *et al.*, 2003; Fossette *et al.*, 2012). Noteworthily, a recent study by Hufnagl *et al.* (2017) argues that model sensitivity, in terms of advection and connectivity estimated with Lagrangian particles, should be assessed prior to validate simulation outcomes. This can be done by using different hydrodynamic models from the same region to perform dispersal and connectivity simulations, instead of accounting only for the absolute values of a single model (Hufnagl *et al.*, 2017). However, cross-model validation is only possible when more than one model exist for the area of interest. When this is not the case, one could alternatively replicate simulations with a single model in order to obtain confidence intervals for the absolute values.

To explore how ocean dynamics influence the biology of marine fishes, physical models need to be coupled with biological information. This is, for instance, pelagic larval duration (Hinckley *et al.*, 1996) or growth rates, but also the occurrence of predators (Grimm and Railsback, 2013). Individual based modelling considers processes such as spatial–temporal variation of spawning activity, egg production and buoyancy, larval dispersal, pelagic larval duration, growth, mortality, and behaviours such as settlement or diel vertical migration (North *et al.*, 2009). An illustration of the realistic approach taken by recent models can be seen in Figure 1 (Peck and Hufnagl, 2012). Information on these parameters can be obtained through field observations, as was done to verify dispersal pathways and recruitment areas of capelin (*Mallotus villosus*) or through experimental approaches to infer, for instance, buoyancy and pelagic larval duration of Atlantic cod's (*Gadus morhua*) early life stages (Wiedmann *et al.*, 2012; Petereit *et al.*, 2014). Metaxas and Saunders (2009) and North *et al.* (2009) detail how such parameters can be obtained, validated and incorporated into ocean models.

Box 1. Eco-evolutionary pressures revealed by biophysical modelling.

Biophysical modelling approaches suggest that the population dynamics—often quantified in terms of recruitment—of broadcast spawners is linked to ecological factors, where currents play a preponderant role. The seminal work of Werner *et al.* (1993) reported a connection between larval dwelling depth and increased retention of Atlantic cod and haddock (*Melanogrammus aeglefinus*) larvae at nursery grounds in George's Bank. This emerges as a result of preferential spawning locations to maximize offspring survival (Werner *et al.*, 1993). After this work, several other studies reported similar patterns: the spawning area of anchovies in the Gulf of Lion correlates with increased larval retention, preventing mortality due to advection (Sabates *et al.*, 2007); Mediterranean bluefin tuna (*Thunnus thynnus*) spawn alongside frontal coastal areas that promote dispersal and retention of drifting larvae in upwelling zones, providing oxygenated and nutrient rich waters (Mariani *et al.*, 2010; Cardinale *et al.*, 2012, Figure 2a–c); Eastern Baltic sprats (*Sprattus sprattus*) benefit from dispersal through wind-forced currents towards nursery grounds that fluctuate in a decadal temporal scale (Scheffer *et al.*, 2005; Hinrichsen *et al.*, 2010; Cardinale *et al.*, 2012); Current-mediated dispersal in winter-spawning flatfishes (order Pleuronectiformes) allows larvae to reach suitable nursery grounds in the Bering Sea (Wilderbuer *et al.*, 2002).

Predator–prey interactions are also relevant for early life stage survival. Another example derived from modelling diel vertical migrations in sprat demonstrates that these behaviours can increase the rate of prey encounter (i.e. Hinrichsen *et al.*, 2010, Figure 2d, e). Reciprocally, predator avoidance strategies are important as shown by the Barents Sea capelin where the locations of the subarctic spawning areas, in coastal waters of Norway and Russia, minimize advection of early life stages to predator-rich areas (Wiedmann *et al.*, 2012).

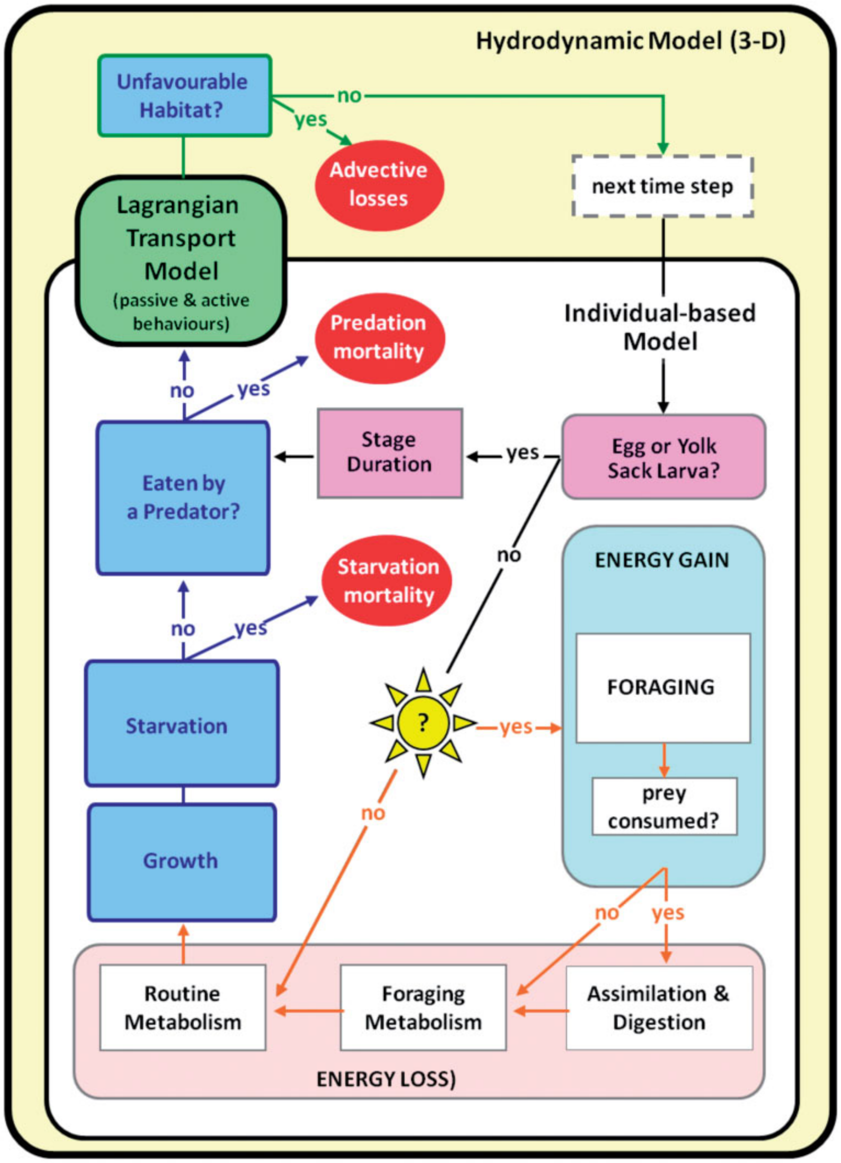

Figure 1. Schematic representation of a standard individual-based biophysical model. Individual-based model (minor polygon) integrated within a 3-D hydrodynamic model (larger polygon), allowing the simulation of ecological interactions within a physical environment. Within the circular-shaped figures, three different sources of early life stages mortality are represented: (i) advective mortality linked to hydrodynamic forcing that results in particles forced to drift towards unsuitable areas; (ii) starvation mortality that relates, amongst others, to the presence/absence of prey at the first feeding stage of fish larvae; (iii) predation mortality, where the target fish species is the target of varying levels of predation that can be modelled (Peck and Hufnagl, 2012). Biological activity is modelled within the IBM and defined by a series of equations that describes, in a first stage, the balance between *energy gain* through exogenous feeding and *energy loss* through several instances of metabolic activities. In a second phase, the net result of this balance is transformed into the variables of *growth* and *starvation threshold.* Note that biological activity is simulated to occur during daytime. This figure was reproduced and edited with permission of the publisher. Specific variables and equations that describe them can be found in the original figure and respective caption in Peck and Hufnagl (2012).

Evolutionary genomics in fisheries research

The last decade's boom in sequencing technologies has provided an unprecedented amount of genomic resources (Glenn, 2011). The expression "next-generation sequencing," hereafter NGS, relates to the development of several sequencing techniques that have increased the resolution of genome scans from few dozens to hundreds of thousands of markers (Mardis, 2008) as well as the identification of specific genomic architecture relevant for species' evolution (Star *et al.*, 2011; Smith *et al.*, 2013; Chain *et al.*, 2014). Marker discovery at a genome-wide scale is performed both by whole genome sequencing and a vast variety of genotyping-by-sequencing methods (Wang *et al.*, 2009; Teer and Mullikin, 2010; Davey *et al.*, 2011; Seehausen *et al.*, 2014). The fact that many populations of marine fishes span large geographic areas, thereby experiencing diverse ecological conditions, make them ideal candidates to study genome-wide impacts of variable

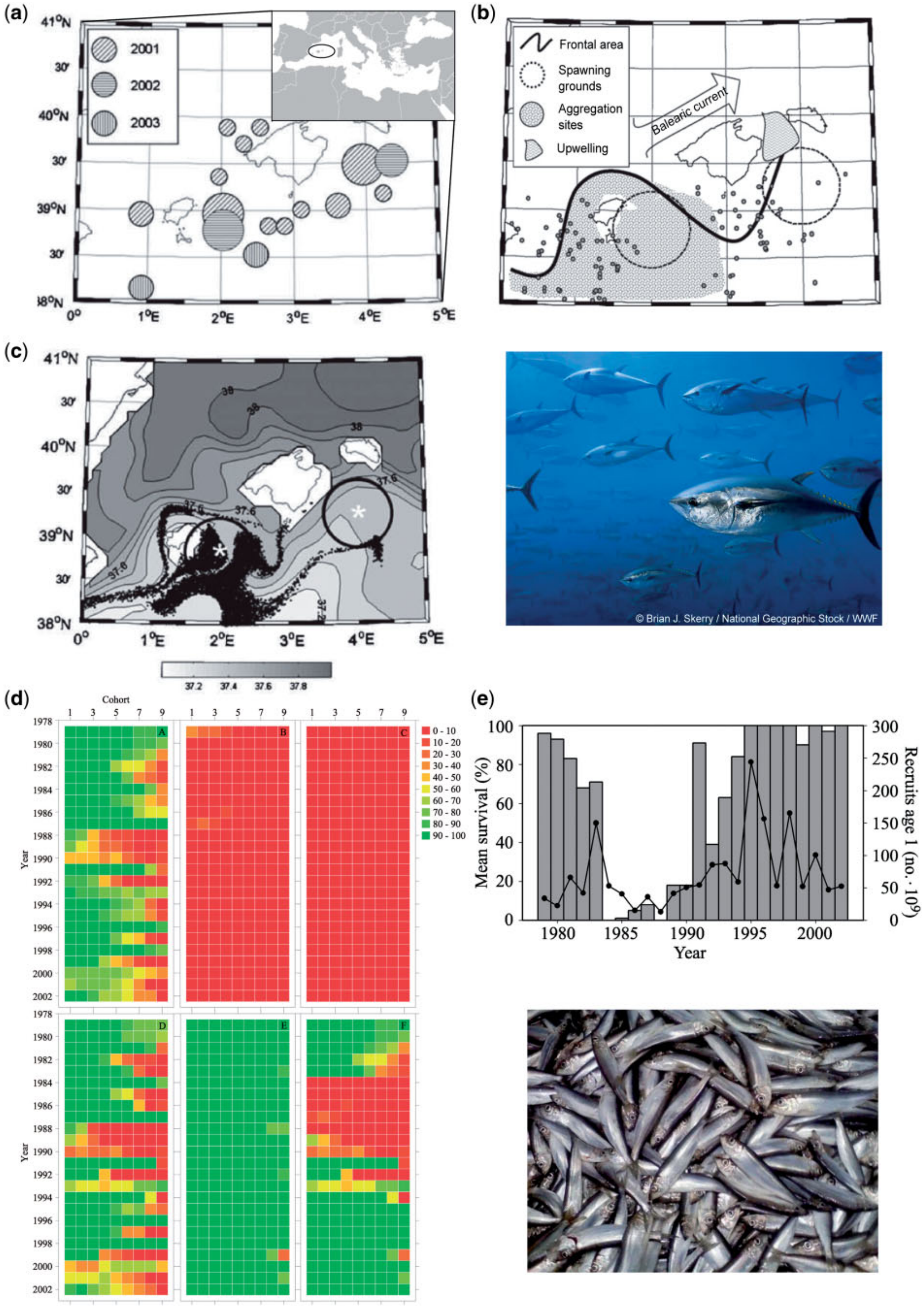

Figure 2. Examples of ecological factors shaping the spawning strategy of Mediterranean bluefin tuna and survival of Baltic Sea sprat's early life stages. Biophysical modelling revealed Mediterranean bluefin tuna's spawning strategy, which relies on the use of frontal areas within the Balearic current to transport and aggregate eggs and larvae in upwelling areas (Mariani *et al.* 2010). (a) Observed distribution of bluefin larvae. (b) Theoretical display of the major oceanic processes likely mediating bluefin tuna's early stages of the life cycle around the Balearic Islands. Dots denote observations from the original study. (c) Model representation of back-tracking of particles released in the aggregation site that matched with the observed spawning area. Ocean models investigating the impact of vertical migration of the Baltic Sea sprat larvae and the abundance of their prey items (*Pseudocalanus acuspus*, *Acartia* spp.) across >10 years on the survival of early life stages of the sprat (Hinrichsen *et al.*, 2010). (d) Representation of the outcome of six simulated scenarios with various combinations of vertical migration of sprat larvae and abundance of prey species (Hinrichsen *et al.*, 2010). Colours represent survival probability of sprat for each of the considered years. (e) Correlation between mean annual larvae survival obtained from Figure 2d-*Panel F*, which includes spatial variation in addition to migration and abundance. This represents the most realistic scenario and matches well the observed recruitment of Baltic Sea sprat ($r = 0.39$, $p < 0.05$).

ecological conditions (Nielsen *et al.*, 2009). The application of genomics to marine fish species has revealed extensive patterns of molecular diversity. For example, partial genomic representations have brought evidence for genomic signature of local adaptation in herring (*Clupea harengus*) through RNA- and exome sequencing (Lamichhaney *et al.*, 2012), have revealed cryptic structure within populations of sea mullet (*Mugil cephalus*; Krück *et al.*, 2013) and hake (*Merluccius merluccius*; Milano *et al.*, 2014); helped to identify growth and maturation-related loci in the common sole (*Solea solea*) through candidate gene approach (Diopere *et al.*, 2013); showed a loss of function of vision-related genes in the half-smooth tongue sole (*Cynoglossus semilaevis*; Chen *et al.*, 2014) or unveiled the genetic basis of temperature adaptation in barramundi (*Lates calcarifer*) by identifying differential expression in genes regulating peptidase activity (Newton *et al.*, 2013). Some of the identified candidate loci are located in genomic regions that exhibit high levels of differentiation when compared across populations along environmental gradients or a geographic range (Sodeland *et al.*, 2016). Genomic islands of divergence are thought to be maintained both by low recombination rates and spatially varying selection (Noor *et al.*, 2001). The identification of those genomic patterns is greatly facilitated by the fact that marine populations tend to exhibit extremely low levels of genome-wide differentiation (Hauser and Carvalho, 2008; Corander *et al.*, 2013). Still, outputs of genome scans must be interpreted carefully. In addition to the classic sampling issues (Lotterhos and Whitlock, 2015) or problems inherent to genomic screening techniques (Lowry *et al.*, 2017), potential pitfalls of NGS refer to properly accounting for demographic effects, which may mask or confound signatures of selection (Bierne *et al.*, 2013; Hoban *et al.*, 2016). Also important to consider is the broad range of mechanisms upon which natural selection relies to leave its signature onto the genomes. Outlier detection might straightforwardly identify genetic variants that have quickly arisen to fixation as a result of a strong and directional selection, the so called hard sweeps (but see Jensen *et al.*, 2016). However, several other mechanisms that do not leave such a stark signature of selection may also be involved, at the molecular level, in the adaptive process. For example, soft sweeps, balancing selection, epigenetic variation or phenotypic plasticity are mechanisms whose detection of their signature might require other statistical tools. The occurrence of these mechanisms in the evolutionary history of marine fishes has been reviewed elsewhere (Bernatchez, 2016).

Merging biophysical models and genomic tools: applications to evolutionary ecology and fisheries management

The identification of ecological selective pressures through modelling of ocean dynamics and the capture of signatures of evolutionary processes through population genomics have largely been presented and interpreted in parallel. Exceptions are perhaps studies that correlate (spatial) genetic variation with environmental cues, i.e. temperature or salinity—environmental correlations (Limborg *et al.*, 2012; Teacher *et al.*, 2013; Benestan *et al.*, 2016). However, those studies do not capture ecological dynamics *per se* and do not explore any putative causality of the relationships beyond the limits offered by correlative approaches. By simulating a diverse set of ecological parameters, biophysical modelling tests multiple scenarios to which information retrieved from the genomes of the natural populations could be weighed upon or accounted for. Here, we will describe two possible workflows to explore the potential of biophysical models as tools to study evolutionary hypotheses in the marine realm. The first relates to the use of biophysical modelling to identify localized selective pressures that may shape species' traits in early life stages of marine fishes. Upon identification, one can screen for the underlying molecular basis of such traits. Those specific genes could then enter monitoring programmes, since loss of genetic variation may reveal changes in selection pressure, which may otherwise not be identified. The second perspective uses biophysical models to test evolutionary hypotheses. In short, the idea is to simulate ecological processes together with genetic information in order to investigate the causes and consequences of local adaptation and connectivity. For example, simulating larval dispersal can provide expectations regarding direction and quantitative estimates of gene flow among putative populations (Benestan *et al.*, 2015). This is crucial because understanding the causes and consequences of the emergence of reproductive barriers assists in the definition of fish stocks but cannot be causally assessed with either biophysical models or genetic tools alone.

Identification of selective pressures and adaptive responses in independently managed stocks

By considering a vast array of ecological parameters, biophysical models are initially designed to explore how their variation affects survival of fish early life stages (Peck and Hufnagl, 2012). It is exactly the effect on survival that allows us to identify selective pressures, as is the case in the example of the common sole. This fish species is widely distributed from the North-East Atlantic Ocean, the Mediterranean and North Seas (Perry *et al.*, 2005). Its life cycle is characterized by a pelagic larval phase followed by a benthic adult phase, facilitated by the ontogenic change that flattens the body of adults. The spawning and larval settling at nursery grounds in the North Sea basin are shaped by the local hydrodynamics of the area. There are six spawning grounds, forming distinct genetically isolated reproductive units (Savina *et al.*, 2010). Like many other marine species, the evolution of distinct spawning areas is largely unknown. Yet, biophysical modelling has shed light on potential mechanisms underlying this genetic structure: Lacroix *et al.* (2013) investigated the influence of hydrodynamics on the connectivity between spawning and nursery grounds as well as the role of larval behaviour on the abundance of recently metamorphosed larvae in the different nursery grounds. Two types of larval behaviours were simulated in their model: vertical migrations and settling delay. The results showed that observed larvae abundance in nursery grounds could be explained both by the hydrodynamics connecting spawning and nursery grounds, as well as larval behaviour. In particular, simulations including "settling delay" correlated well with abundance from records of fish stock (FAO, 2001)—further suggesting that delayed behaviour increases the settling success in the nursery grounds. Interestingly, modelled larval abundance was not consistent across nursery grounds (Lacroix *et al.*, 2013). This suggests that strategies that facilitate success in the transport and settlement of larvae are, to some extent, population-specific, i.e. genetically encoded and locally adapted. It seems that settling mechanisms maintain the genetic structure and genetic diversity, thereby maintaining the adaptive potential of the common sole stocks in the North Sea. Similar observations may be extended to another flatfish species (*Pleuronectes platessa*) that inhabits the same geographical area and possibly shares the same coastal nursery grounds (Hufnagl *et al.*, 2013).

The identification of loci differentially under selection strengthens the arguments of distinct stocks and is therefore relevant for management (Hemmer-Hansen *et al.*, 2014a). Fisheries management often refers to genetic diversity as a genome-wide characteristic. However, increased genomic resolution tends to reveal particular regions to be specific targets of natural selection (Nosil *et al.*, 2009; Feulner *et al.*, 2015; Sodeland *et al.*, 2016). In the case of the common sole, one could assume that selection for settling behaviour leaves a stronger signal in the genome than produced by genetic drift due to population structure. It is then possible to estimate genome-wide neutral differentiation between locations, and expect genomic regions putatively linked to settling behaviour to emerge as candidate loci under selection (Narum and Hess, 2011; Diopere *et al.*, 2017). That sort of genetic variants have shown to be involved in the molecular basis of certain behavioural traits in marine species, such as the adult migration of the anadromous steelhead trout (Hess *et al.*, 2016), benthic adaptation and schooling behaviour in three-spined sticklebacks (Greenwood *et al.*, 2013; Erickson *et al.*, 2016), and age variation at which Atlantic salmon migrates to the sea (Johnston *et al.*, 2014).

The possible identification of genomic regions of adaptive divergence in the common sole genome would also be important to enhance predictions of the species response to the accentuated impact of climate change in the North Sea (Perry *et al.*, 2005). Because this species is undergoing a southward shift of its distribution range (Engelhard *et al.*, 2011), linking genetic variation involved in settling behaviour with any type of characteristic of the settling environment could permit the identification of suitable habitat areas outside the native range.

The identification of putative strategy-specific genetic variation would allow for the development of genetic markers to be screened along time series or at various geographic scales. For fisheries, this would translate into a tool to monitor ecologically relevant adaptive genetic diversity and also to prevent mismatches between populations and habitats in the cases where translocations would be a management method. Biophysical modelling, tissue sampling for DNA extraction and sequencing of random genetic markers are common procedures in management of species with well described biology (Ferguson, 1994; Palsbøll *et al.*, 2007). They are used to delimitate boundaries, whether those of stocks to exploit or marine protected areas to preserve (Palumbi, 2003). This means that including screens of adaptive genetic diversity would not add substantial efforts but the benefits could be high. For instance, the detection of shifts in the allelic frequencies of functional variants during monitoring programmes could alert managers for changes in selective pressures, therefore prompting for a rapid response.

Connectivity and maintenance of evolutionary potential in near panmictic species

Genetics—and now genomics—contribute to the detection, definition and establishment of "populations" in marine species (Dunlop *et al.*, 2009; ICES, 2015). The absence of conspicuous barriers to free movements of individuals does not necessarily imply the existence of a single reproductive unit nor that of a genetically homogenous stock (Hauser and Carvalho, 2008; Cowen and Sponaugle, 2009). Genetic variation may evolve at finer geographic scales due to drift and early emergence of sub-populations, due to local adaptation, or the existence of cryptic species (Hemmer-Hansen *et al.*, 2013; Breusing *et al.*, 2016; Picq *et al.*, 2016). Overlooking the possibility of these scenarios may bring irreversible damage to the sustainability of exploited species (Brodersen and Seehausen, 2014). A critical example is perhaps that of the North Sea cod (Hutchinson, 2008). In the early 21st century, genetic analyses of archived otolith samples revealed that the single population stock was in fact formed by several genetically distinct sub-populations (Hutchinson *et al.*, 2003). Further investigations revealed that decades of fishing pressure preceding the 1960s/1970s collapse have disproportionally affected each of the sub-populations and likely compromised a sustainable exploitation (Hutchinson, 2008).

Suggestions have been made to increase the resolution of genomic analyses to employ a holistic approach using neutral, selective and hitchhiker loci to assess connectivity (Gagnaire *et al.*, 2015). For all marine species, the primary challenge is to understand how the physical movement of individuals shapes and maintains the spatial distribution of genetic diversity. For many exploited species, this is inherent to the knowledge gap regarding spatial–temporal occurrence of spawning events as well as sampling location (i.e. spawning, nursery or foraging grounds). By incorporating genetic information in simulations of physical dispersal/movement and performing *in silico* capture of individuals—mimicking sample collection—physical models are powerful tools to explore hypothetical scenarios: because hydrodynamic models are built upon time series of data that span a range of environmental regimes, distribution of genetic variation can be simulated under natural conditions. If expanded to larger, open-ocean systems, seascape genetics provides the initial framework to investigate putative associations between ocean environment and distribution of genetic diversity (Selkoe *et al.*, 2008). However, as the use of individual-based modelling and next generation sequencing was, at that time, not considered, understanding how dispersal and connectivity could shape the evolution and distribution of adaptive genetic variation was not approachable. With the next example we will suggest possible ways to integrate the recent advances in the seascape framework.

The Antarctic toothfish (*Dissostichus mawsoni*) is a member of the notothenioid lineage that inhabits Austral waters. Despite a rapid emergence as economically important species, knowledge of its ecology, dynamics and structure in the Ross Sea (and elsewhere in the Antarctic waters) is scarce (Ainley *et al.*, 2013; Abrams *et al.*, 2016). The apparent single panmictic population is spread across a large geographical area, with the spawning grounds located in the North Banks region (Hanchet *et al.*, 2008). Ocean currents in the Ross Sea connect pelagic larvae to the nursery grounds along the Antarctic continental shelf where juveniles feed. Adults then migrate to the Ross Sea to forage (Hanchet *et al.*, 2008). Ashford *et al.* (2012) attempted to validate the connectivity hypothesis between spawning, nursery, and foraging grounds by combining results of a biological (otolith chemistry) and a physical oceanography (modelling and Lagrangian particle tracking) source. The wide geographical distribution of the species is intriguing: adults, which drift with currents, are found in areas that in theory are inaccessible, considering physiological characteristics of the species. Likewise, the same physiological characteristics would impede adults to swim from those locations back to the spawning grounds. Dispersal simulations provided two important insights. First, the complete life cycle of this species is apparently supported by the circulation system of the Ross Sea (Ross Gyre), where ontogenic changes in buoyancy may have facilitated the adaptation to regional conditions after the occupation of an empty niche around Antarctica (Ainley *et al.*, 2013). The negative buoyancy in juveniles prevents dispersal away from important nursery grounds and the neutral buoyancy in adults facilitates the roaming between foraging and spawning grounds (Ashford *et al.*, 2012). Second, the study suggested the existence of an alternative life cycle with some individuals using a narrower geographic range than others. Under the actual hydrodynamic conditions, this strategy is predicted to have marginal implications on the dynamics of the population occupying the Ross Gyre (Ashford *et al.*, 2012). However, conditions changing, the alternative life cycle could gain a key role for the viability of the species. While the modelling approach successfully identified two distinct strategies, it has yet to show their significance to the overall population dynamics. Whether this represents distinct but yet undetected spawning grounds, two distinct strategies within a single panmictic population or both is largely unknown. Since the species is managed as a single stock in this area, clarifying the contribution of each strategy to the overall population dynamics could result in implementing novel fisheries regulations.

For this specific example, we envision two possible approaches to explore the contribution of each strategy to the population dynamics and possible impacts to the species management. The first includes the simulation of two genetically distinct foraging grounds, where virtual Lagrangian drifters mimicking the current-driven dispersal of adults towards spawning would be incorporated. In this case, one must consider (i) Mendelian inheritance, (ii) fixed mutation rate, and (iii) equal starting heterozygosities of the genetic variants employed to discriminate foraging grounds in the simulations. Also, one must assume that foraging grounds segregate into distinct spawning areas and that the gene flow between them, i.e. proxy for number of individuals belonging to one area that went to reproduce in the other, is constant across generations. Under these conditions, the model could be run for several generations across oceanographic scenarios that include the temporal and spatial natural variation the local currents to explore the likelihood of the two foraging strategies to evolve into two distinct populations. For instance, one could observe in how many generations oceanographic conditions would lead to a spatial, temporal or spatial–temporal displacement of adult individuals in the spawning area. The second approach that could be used includes genome-wide screens of individuals of the Ross Sea population to identify candidate loci under selection assuming a single panmictic population (Antao *et al.*, 2008; Foll and Gaggiotti, 2008). Upon identification, the frequencies of candidate loci would be correlated with environmental variables such as temperature, salinity or current speed, provided by hydrographic modelling of the region. Lastly, genetic variants could be incorporated into individual-based models to explore the performance of genetic variants under different ocean regimes, considering, for instance, each variant with a specific value of advection loss (e.g. Figure 3). To mitigate the effect of stochasticity, one could either perform replicated runs—considering multiple generations—with exactly the same parameters and correct the average of advective loss by the variance obtained across replicates or test different hydrodynamic models (if available) of the region of interest (Hufnagl *et al.*, 2017). In theory, advective loss could be correlated with estimates of effective population size obtained from genetic data for instance.

The approaches described here would provide two levels of information to fisheries management. The first information would be an overview of possible environmental factors influencing the stock dynamics: considering the importance of ocean currents to fish migration in the area, it is relevant to understand how regime shifts could impact the stock's structure. In the case of regime shifts leading to spatial or temporal fragmentation of the stock, management strategies would respond by partitioning the fishing activity to avoid disproportional harvesting of one stock over the other. The second information is critical to estimate, from a genetic perspective, the resilience of the stock to regime shifts. A direct management practice would be to *in silico* evaluate the impact of stock partitioning and likewise implementation of different quotas either on a spatial or on a temporal scale. When information is scare, the overarching goal is to preserve all levels of diversity, until the dynamics of ecosystems or the natural history of the target species are better understood.

Overall, the proposed framework can be summarized as follows (Figure 3a–e): (i) sum up the basic knowledge about the life cycle of the target species, as well as the hydrodynamic features of the region that it inhabits. If knowledge gaps exist, regarding, for instance, the spawning grounds, the nursery grounds and the sensitivity of early life stages to oceanographic processes—such as currents or upwelling events—they can be identified with ocean models. The availability of Ocean Global Circulation Models developed for several regions of the World facilitates the choice of specific hydrodynamic models (reviewed in Fossette *et al.*, 2012). (ii) To test how different ecological factors might influence the survival of larvae, one could simulate variation of speculative key traits (one trait, multiple variants) that confer fitness advantage in variable ecological pressures. For example, consider a trait linked to advection such as *pelagic larval duration*, and respective variants A, B, and C (Figure 3c). A could be associated with short, B average and C long planktonic phase respectively. These could be incorporated into the biophysical model by varying advection time of each variant and quantify abundance, at the end of the simulations. Predicted abundance obtained from the model would then be correlated with observed abundance (based on recruitment indices obtained from fisheries data, for instant). Significant correlations would support the role of the trait in responding to oceanic variation and being under oceanic current-mediated selection. (iii) Sampling the target species for DNA, one would then perform genome-wide screens to obtain genomic markers (Figure 3d). In a first stage, those would be used to characterize population structure and estimate levels of neutral differentiation. In a second stage, candidate loci under selection could be identified to afterwards be compared against publicly available genomes.

Correlation between simulated trait variation and its putative genetic basis could then be tested in diverse ways. Individuals could, for instance, be sampled from natural populations at nursery grounds under conditions similar to those modelled and screened the frequency of identified genetic variants. Another possibility would be to collect the eggs of target species and rear them under manipulated laboratory conditions: different salinities or temperatures could be tested to verify the variation in egg buoyancy or growth rates; the importance of size at first feeding check could be tested by exposing reared juveniles to food items of different sizes. Individuals whose traits have varied under manipulated conditions would then be screened for the presence of identified genetic variants.

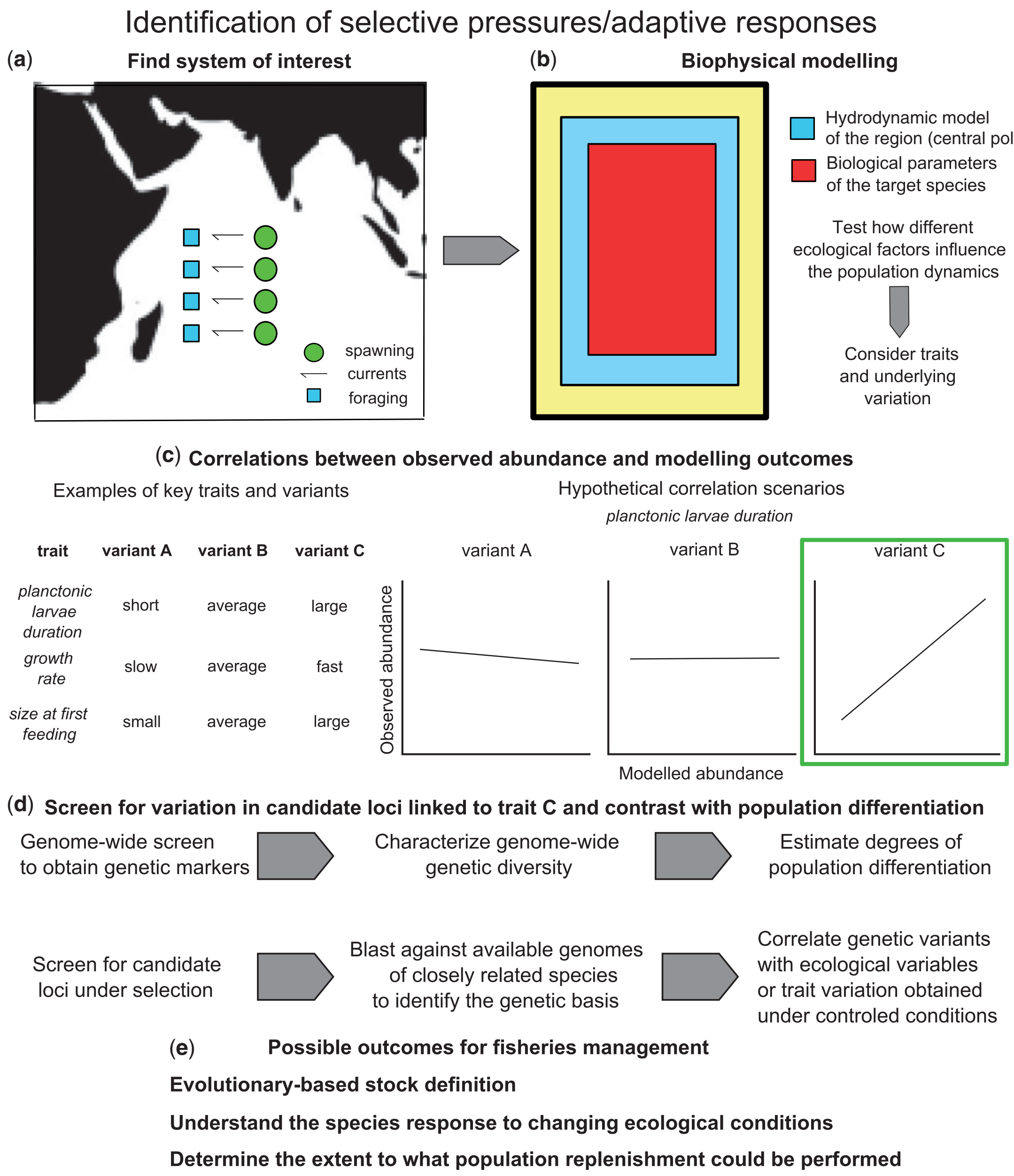

Figure 3. Framework to integrate evolutionary theory into biophysical modelling. Here, the use of biophysical models is highlighted to identify selective pressures in the target system, and work all the way down to the identification of a possible genetic-basis of the adaptive response. Briefly, the first step is to identify the system of interest. Biophysical modelling should then take into consideration the oceanic processes that occur in the target area, which assumes the incorporation of already existing oceanic models as well as biological traits of the model organism. Trait variation can be incorporated either by observations (i) from the field, i.e. seasonality in spawning activity, (ii) inferred from laboratory experiments, i.e. variation in buoyancy, or (iii) simulated within the IBM via manipulation of key variables, i.e. those present in Figure 1. The identification of a selective pressure also permits one to formulate *a priori* expectations regarding candidate loci, facilitating interpretation of F_{ST} outlier approaches when variants cannot be mapped to known functional regions.

Incorporating genetic information that underlies the basis of trait variation in management practices, i.e. performing genetic screens of fish stocks, would open new avenues in evolutionary-based fisheries management. It would facilitate predictions on how shifts in ecological conditions would impact the dynamics of fishing stocks, as well as facilitate measures to replenish species or populations abundances.

Challenges to overcome

This manuscript aims at re-affirming the importance of interdisciplinary collaboration between biophysical modellers and evolutionary biologists, in particular population geneticists. Because management decisions have wide implications not only for the environment but also to the society, it is important to carefully consider the caveats of each approach: e.g. the stochasticity inherent to biophysical modelling, which requires an assessment of model sensitivity to mitigate its effects, or the assumptions of population genetic theories, of which the complexity of marine populations and the signatures of natural selection left in the genome of marine species seem to frequently defy (Hauser and Carvalho, 2008; Selkoe *et al.*, 2008; Bernatchez, 2016; Hufnagl *et al.*, 2017). However, to jointly interpret the outcomes of the combined methods is also a way to reduce the errors inherent to each approach. Identifying the key selective pressures together with the genes directly evolving under those pressures confer robustness to the modelling and population genomic results alike (Figure 3). Furthermore, it allows for the formulation of stronger assumptions than non-causal environmental correlations. Regarding stock identification and connectivity, what are thought to be artefacts of biophysical modelling can be used as hypothesis-driven scenarios and tested for validation/refutation with genetic tools, or *vice versa*.

Another important challenge is the high likelihood of phenotypic variation to be governed by multiple genes of small effect size. In those cases, it is suggested to invest in denser genomic screens, larger sample sizes, and extend the analyses to within-population comparisons of genetic and phenotypic variation (Gagnaire and Gaggiotti, 2016). Methodology based on polygenic scoring to estimate the contribution of multiple candidate loci to the observed trait variation, particularly designed to detect polygenic selection in marine populations would also be an approach to follow (Gagnaire and Gaggiotti, 2016).

On the future of evolutionary-based fisheries management

By coupling ecological and biological parameters, biophysical models explore the interaction of biological entities with their surrounding environments under simulations of realistic ecological conditions. Although they are mainly applied in a purely ecological framework, here we have suggested how they can further be used as *in silico* tools in evolutionary ecology to enhance fisheries management and provide estimates of adaptive potential. Understanding stock resilience has recently gained increasing importance because of rapid ocean changes, including ocean acidification (Sunday *et al.*, 2014), and raising temperatures (Harley *et al.*, 2006), with possible influence on major ocean currents (Broecker, 1997). The multitude of selective pressures acting on fish stocks calls for upscaling the traditional management strategies to a level where the adaptation to selective pressures and consequence for stock dynamics is considered. Because trait/genetic variation are a key aspects of a species' evolutionary potential, their preservation should be seriously considered in management strategies. As the complete set of ecological conditions is impossible to reproduce in controlled environments and most of the marine exploited species are far from being model experimental organisms, we argue that the use of biophysical models to create and test evolutionary hypotheses is the first step to better understand organism–environment interactions.

Acknowledgements

The authors would like to thank T. B. H. Reusch and D. Schmidt for reviewing earlier versions of the manuscript. We would also like to thank the editor, Mikko Heino, and two anonymous reviewers for the comments and suggestions that helped improve the manuscript.

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Handling editor: Mikko Heino