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Author for correspondence:

Amanda Xuereb

e-mail: amanda.xuereb.1@ulaval.ca

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Individual-based eco-evolutionary models for understanding adaptation in changing seas

Amanda Xuereb¹, Quentin Rougemont², Peter Tiffin³, Huijie Xue⁴ and Megan Phifer-Rixey⁵

¹Institut de Biologie Intégrative et des Systèmes, Département de Biologie, Université Laval, 3050 Avenue de la Médecine, Québec, Québec, Canada G1 V 0A6

²CEFE, Centre d'Ecologie Fonctionnelle et Evolutive UMR 5175, CNRS, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France

³Department of Plant and Microbial Biology, University of Minnesota, 1479 Gortner Avenue, Saint Paul, MN 55108, USA

⁴School of Marine Sciences, University of Maine, 5706 Aubert Hall, Orono, ME 04469-5706, USA

⁵Department of Biology, Monmouth University, 400 Cedar Avenue, West Long Branch, NJ, USA

AX, 0000-0002-3975-2299; HX, 0000-0003-0738-4978

As climate change threatens species' persistence, predicting the potential for species to adapt to rapidly changing environments is imperative for the development of effective conservation strategies. Eco-evolutionary individual-based models (IBMs) can be useful tools for achieving this objective. We performed a literature review to identify studies that apply these tools in marine systems. Our survey suggested that this is an emerging area of research fuelled in part by developments in modelling frameworks that allow simulation of increasingly complex ecological, genetic and demographic processes. The studies we identified illustrate the promise of this approach and advance our understanding of the capacity for adaptation to outpace climate change. These studies also identify limitations of current models and opportunities for further development. We discuss three main topics that emerged across studies: (i) effects of genetic architecture and non-genetic responses on adaptive potential; (ii) capacity for gene flow to facilitate rapid adaptation; and (iii) impacts of multiple stressors on persistence. Finally, we demonstrate the approach using simple simulations and provide a framework for users to explore eco-evolutionary IBMs as tools for understanding adaptation in changing seas.

1. Introduction

Impacts of climate change are already being felt in both terrestrial and marine ecosystems [1]. In some cases, extreme thermal conditions have had devastating effects on biodiversity, including recurring massive coral bleaching events [2] and the collapse of fisheries [3]. While challenging, predicting responses to climate change, and in turn implementing effective mitigation strategies, is increasingly urgent as the rate of climate change accelerates. Species show a range of physiological and ecological responses to changing environments, including alterations to growth and metabolism [4,5], phenology [6] and biotic interactions [7], which can translate into shifts in the distribution and abundance of populations [8,9]. Species may also adapt to changes in local conditions [10], and the potential for adaptation will depend on genetic variation in local populations and the scale and degree of gene flow [11–13].

Model-based approaches can be valuable for exploring possible responses to environmental change. For example, species distribution models (SDMs) are used to infer geographical distributions of organisms based on correlations between species' occurrence and biotic or abiotic predictors [14]. In climate envelope models, a type of SDM, distributions are inferred based on associations

with bioclimatic variables such as temperature or precipitation (a given species' potential climate niche), and predictions of how contemporary ranges and abundance might shift in the future can be made using projections of available niche space under climate change scenarios (e.g. [15]). An important limitation of this type of approach is that it lacks the integration of biological mechanisms (e.g. physiology, dispersal, species interactions) underlying species' range dynamics [16]. Evolutionary responses can mediate the impact of climate change on distribution patterns and abundance [17], but mechanisms of adaptation are generally excluded in SDM-based approaches [18]. Eco-evolutionary models, which incorporate ecological and evolutionary processes, can be powerful tools for predicting how adaptation might affect persistence under climate change [19,20]. In particular, individual-based models (IBMs) provide an adaptable framework for simulating complex ecological and evolutionary processes, with trait variation and demographic stochasticity modelled at the individual level [21,22]. While computational demands of IBM approaches can be significant, the development of efficient, flexible and user-friendly toolkits such as SLiM [23–25] have made large-scale eco-evolutionary IBM approaches more widely accessible. For example, the tree-sequence recording method [26], now implemented in SLiM3 [27], simplifies the structure of genealogical information storage, greatly improving the speed of forward simulations.

Here, we explore the use of eco-evolutionary IBMs to predict adaptive responses of marine species to climate change. We reviewed the literature to identify studies that have used this approach, and identified key insights as well as opportunities for further development. We focused on three topics that emerged: (i) effects of genetic architecture and non-genetic responses; (ii) the capacity for gene flow to enhance adaptive potential; and (iii) the consideration of multiple stressors in predictions of species' persistence. Finally, we implemented genetically and spatially explicit eco-evolutionary IBMs to demonstrate how hypotheses regarding impacts of multiple stressors could be tested. Our intent is not to capture the biological reality of any specific system, but rather to exemplify the use of eco-evolutionary IBMs in this context and provide an accessible framework that can be applied to explore impacts of climate change and other challenges in diverse systems.

2. Literature search

We searched the ISI Web of Science and PubMed databases to identify studies that used IBMs to simulate marine eco-evolutionary dynamics in the context of climate change, scanning titles, abstracts and keywords in articles published after 2005 for combinations of the terms 'individual-based model', 'marine', 'sea', 'ocean', 'evolution', 'adaptation' and 'simulation' (see electronic supplementary material, S1 for full description of methods). While researchers have used diverse approaches to model potential impacts of climate change in marine systems (e.g. dynamic energy budget modelling or population growth modelling), we found relatively few studies that used eco-evolutionary IBMs to model adaptation. Among the 21 articles that passed initial filtering, 10 focused on impacts of fishing and/or reserves (electronic supplementary material, S1). While not the focus of this review, the approaches parallel those used to predict responses to climate change,

including forecasting responses to human-induced pressures and modelling evolutionary impacts of fishery management strategies and multiple stressors (e.g. [28]). Five additional studies were unrelated to climate change [29–31]. From the remaining six studies, we extracted criteria that illustrate how eco-evolutionary IBMs are currently parametrized and identify possible gaps in their implementation in the context of adaptation to climate change (table 1). Three papers were genetically explicit, meaning individual loci were modelled [32–34]. Taxonomic representation was highest among coral and fishes (table 1; electronic supplementary material, S1), systems that are historically well studied. Notably, most papers provide publicly accessible code; several are implemented in SLiM [23–25], which has a graphical user interface (GUI), or R, which is a familiar tool for many biologists (table 1). The accessibility of scripts and modelling tools means that simulations can be readily modified for different systems.

Although the limited number of studies identified prevents broad generalizations, they show how an eco-evolutionary IBM approach can be applied to predict the potential for adaptation to changing environments. One clear application is to compare outcomes across different scenarios to better understand the implications of specific parameters. Most studies explored assumptions regarding multiple aspects of the model, including varying climate projections, genetic architecture and dispersal (table 1). One study compared effects of various factors (e.g. juvenile mortality, rate of environmental change, migration) on adaptive potential, and found that the rate of temperature change, initial temperatures and influx of warm-adapted recruits were especially important in determining persistence of coral populations [34]. Another focused on the impact of varying climate projections on persistence of coral (*A. hyacinthus*) populations [32] and found that rapid evolution of heat tolerance allowed for population persistence only under mild warming scenarios, and the speed of adaptation depended on the number of loci and population growth rate. These studies demonstrate how IBMs can be used to determine the importance of particular factors on evolutionary trajectories.

Limitations of simplifying assumptions were also a common theme, with calls to interpret results cautiously. Studies highlighted critical issues that need to be addressed, particularly if results would be used to inform management and conservation. Three themes emerged across studies, which we discuss further: (i) the need to better understand effects of genetic architecture and non-genetic responses on adaptation [32–35]; (ii) the need for better integration of dispersal and connectivity [32,34,36]; and (iii) the need to consider multiple stressors given that climate change will likely be accompanied by other challenges [34] and impacts on multiple traits [37] (table 2).

3. Genetic architecture and non-genetic responses

Genetically explicit eco-evolutionary IBMs provide a powerful set of tools for modelling complex chromosome structures, over a range of parameters (figure 1*a*; [24,25]). The studies uncovered in our literature search that used this approach focused on simulating polygenic traits [32–34]. For example, in [32], simulations were parametrized based on previous empirical work identifying 114 SNPs associated with thermal tolerance

Table 1. Key characteristics of studies using eco-evolutionary IBMs in the context of marine climate change.

citation	major goal	taxa	genetic architecture	dispersal in space	dispersal in time	other parameters varied	code availability
[32]	predict adaptive potential	coral: <i>Acropora hyacinthus</i>	polygenic; 10–1000 loci	closed population, tested AGF rates	constant	climate model, initial population size, intrinsic population growth rate	details may be requested from authors
[33]	predict adaptive potential	coral: <i>Acropora millepora</i>	polygenic; 10; 100 loci	discrete patches, migration rates inferred from genetic data; tested biophysical and no-migration model	constant	heritability, breadth of thermal tolerance, mutation rate, N_e	SLiM (2): Github https://github.com/zdon/Adaptive-pathways-of-coral-populations-on-the-Great-Barrier-Reef
[34]	predict adaptive potential	coral: <i>Acropora</i>	polygenic; 10; 100 loci	discrete patches, biophysical model; tested no-migration model	constant	climate model, juvenile mortality, environmental noise, width of fitness function, mutation rate and effect size, reef size	SLiM (3.3): Github https://github.com/zdon/CoralTriangle_SLiM_model
[35]	predict impact of climate change on migratory species	migratory marine taxa (e.g. fish)	not explicit; (genetic variance)	closed population of philopatric adults, focuses on migration timing	NA	rates of change and variability in optimal migration timing, genetic inheritance, plasticity, bioclimate envelope size	R: code in electronic supplementary material
[36]	predict impact of network structure on adaptive potential	generic, application to sedentary taxa (e.g. coral)	not explicit; (genetic variance)	discrete patches, variable network openness	constant	levels of openness, temperature regime, growth model	Numpy: Zenodo https://zenodo.org/record/4620329#.YQLuHB0p8BI
[37]	predict impact of climate change on life-history strategy and population dynamics	masu salmon: <i>Oncorhynchus masou masou</i>	not explicit; (genetic variance)	closed system, focuses on migratory dynamics	NA	rate of climate change, the rate of evolution in the key trait, body size	C: Github https://github.com/lhorita/Horita-et-al-Eco-evolutionary-dynamics-may-show-an-irreversible-regime-shift

Table 2. Summary of key opportunities that emerged from studies using eco-evolutionary IBMs to address adaptation to climate change in marine systems.

1. genetic architecture and non-genetic responses	—evaluate sensitivity of model outcomes to parameter values (e.g. number of loci, recombination rate)
	—predict impacts of fluctuating environments on evolution of plasticity
	—test hypotheses about how combined effects (and trade-offs) of plastic and genetic responses influence adaptation
2. gene flow and adaptive potential	—identify populations for which immigration from stress-adapted populations is (un)likely
	—assess conservation interventions (e.g. assisted gene flow)
	—test hypotheses about climate-driven shifts in connectivity on adaptive potential and fitness
3. multiple stressors	—generate expectations for effects of multiple stressors on adaptive potential and fitness
	—incorporate effects of overlapping generations, complex age structures and mating schemes, demographic stochasticity, spatio-temporally varying selection, multiple environmental layers and spatial interactions

in tabletop corals (*Acropora hyacinthus*) [39], but they tested the sensitivity of outcomes to the number of loci underlying adaptive traits. They showed that extinction of *A. hyacinthus* populations was likely, even under less extreme warming projections, when traits conferring heat tolerance were controlled by a very large number of loci (>400), while fewer loci permitted more rapid adaptation and slower population declines.

In addition to the number of loci, the distribution of their effect sizes could impact evolutionary outcomes. Models that explored variation in this parameter found little effect on overall outcomes for coral populations [33,34], but that may not be true in all systems. Moreover, simulations also showed that the proportion of variance explained by those genes (i.e. heritability) may also be important: while lower heritability reduced the efficiency of local adaptation and mean fitness, it did not diminish metapopulation persistence [33]. Together, these studies highlight the utility of IBMs to better understand how sensitive predictions of climate change outcomes are to variation in parameter values related to genetic architecture, many of which are not fully understood in most systems.

Phenotypic (plastic) shifts in response to changes in local environments have been documented in marine species [40,41] and their impacts on adaptive evolution are complex [9,12,42]. Few studies have incorporated plasticity directly into eco-evolutionary IBMs of adaptation to climate change. In one example, Anderson *et al.* [35] modelled both genetic and phenotypic climate-driven shifts in migration timing in a highly migratory marine species. Although this study focused on a closed population, their model showed that plastic responses reduced the probability of adaptation when genetic variability was low [35]. IBMs of masu salmon (*Oncorhynchus masou masou*), in which life-history strategies (resident versus migrator) are determined by juvenile body size, showed that as climate change impacts growth, adjusting migratory behaviour based on learned relative status could alleviate effects on population dynamics when adaptation to a new size threshold is slow [37]. Matz *et al.* [33] also incorporated some degree of plasticity by varying the range of non-heritable thermal tolerances: broader tolerance reduced the efficacy of selection, but increased population mean fitness.

(a) Opportunities for development

The genetically explicit IBM framework allows for complex genome architectures to be incorporated, including different

regions (e.g. introns, exons, non-coding elements), types of mutations (beneficial, deleterious, neutral) and genome-wide variation in recombination rates (figure 1a). Eco-evolutionary IBMs, together with theoretical studies, provide an opportunity for testing model sensitivity to underlying architectures of fitness traits, which can be difficult to characterize empirically [43]. Beyond varying the number of loci, genetically explicit IBMs can also be used to test the impact of various distributions of mutational effects, including deleterious mutations [24]. This could be important to consider if, for instance, alleles are hypothesized to be beneficial in one context but may be deleterious in another [31]. Moreover, this approach allows for modelling more complex chromosome architectures, including regions of suppressed recombination and other structural variants, which have been associated with local adaptation in marine species [44–46]. Genetically explicit IBMs can also incorporate epistatic interactions [24], the effects of which have not yet been explored in eco-evolutionary IBMs of marine climate change. The tree-sequence recording method may be advantageous for more efficiently modelling increasing genome complexity, although relative gains in computational performance will depend on the architecture of genomes modelled [27]. Finally, integrating plasticity in eco-evolutionary models of climate change adaptation is so far limited [22] and the diversity of mechanisms underlying plastic responses have yet to be incorporated [12,42,47]. Together with empirical studies, models that consider how environmental fluctuations influence the evolution of phenotypic plasticity [48], and the combined effects of plastic and genetic responses and trade-offs therein [49], can advance our understanding of the mechanisms that influence adaptive evolution and species' persistence.

4. Gene flow and adaptive potential

Eco-evolutionary IBMs have the power to incorporate gene flow, which can have important consequences on adaptive potential, in a way that reflects biological reality. Gene flow can homogenize populations, and the balance between gene flow and selection can influence the capacity for adaptation [50,51]. High levels of gene flow could result in local collapse via influx of maladaptive migrants [52]. Alternatively, gene flow can support rapid adaptation by transporting beneficial alleles among populations [53].

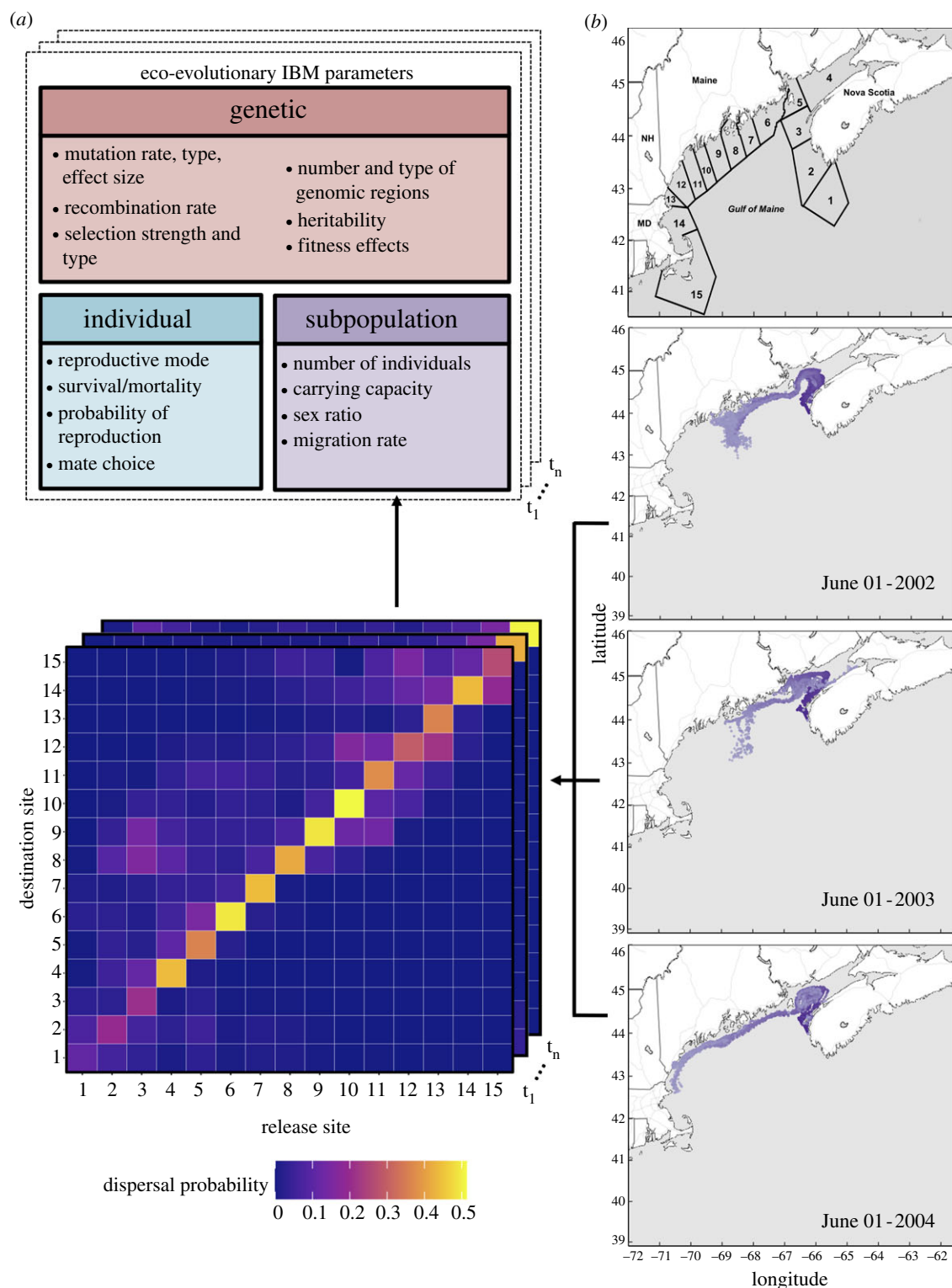


Figure 1. (a) Parameters in genetically explicit eco-evolutionary IBMs such as SLiM at three levels: genetic parameters include the rate, type, and effect size of mutations, recombination rate, strength and type of selection, number and type of genomic regions, heritability and fitness effects; individuals have defined reproductive modes (e.g. biparental, selfing), survival or mortality rates, reproductive success and mate choice (e.g. random, preference-based); subpopulations can be characterized by the number of individuals, carrying capacity, sex ratio and migration rates; (b) map of 15 zones (adapted from [38]) and predicted trajectories from a biophysical model of larval dispersal in the Gulf of Maine for 3 years (2002–2004), showing daily positions up to 60 days following release (on 1 June) from zone 3 (see [38] for details); (c) connectivity matrices of dispersal probabilities (proportion of larvae released from each source that settle in each destination) between zones for each year of the biophysical model (t_1 to t_n), which can be used to define migration rates in eco-evolutionary IBMs and can be updated through time. (Online version in colour.)

Immigration-based adaptation may be critical for accelerating adaptive responses [54,55], especially when populations occupy diverse environments and thus may harbour standing genetic variation for resistance to stressful conditions (e.g. [39,56,57]).

The spatial configuration of dispersal networks can impact adaptation by shaping the distribution of adaptive genetic variation among subpopulations [36]. For many marine systems, the scale and degree of dispersal are governed by physical oceanography [58]. Ocean currents can transport propagules

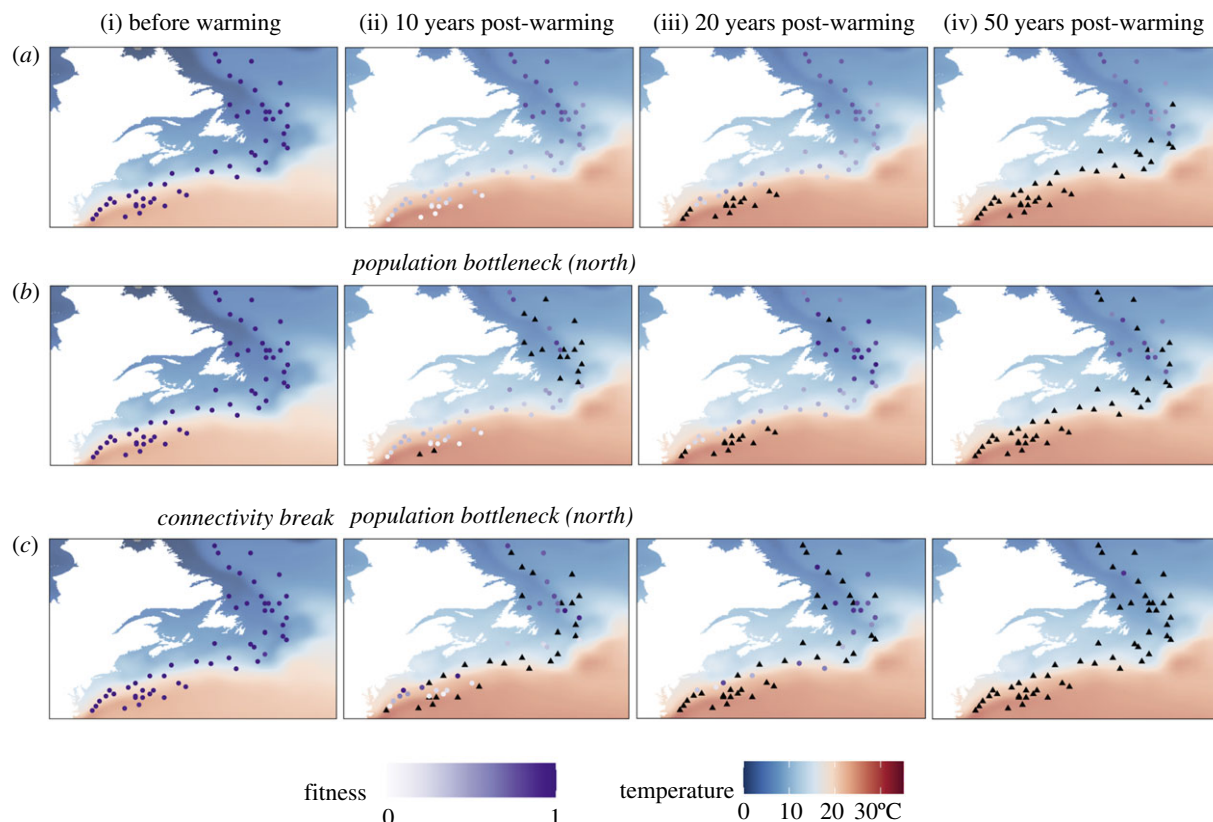


Figure 2. Fitness across 54 hypothetical populations in the western Atlantic Ocean prior to warming (i), and after 10, 20, and 50 years of warming (ii–iv) for three scenarios: (a) warming only; (b) a bottleneck in northern populations occurs immediately prior to onset of warming; and (c) northern and southern populations are disconnected, followed by a bottleneck and warming as in (b). Fitness is computed as the difference between an individual's phenotype and the temperature at its location [34]. Triangles represent extinct populations (mean fitness < 0; phenotype and temperature mismatch). (Online version in colour.)

over broad spatial scales [59], while other features (e.g. coastal topography, eddies and seasonal fronts) may act as barriers, restricting dispersal and increasing local retention [60–62]. Oceanographic features are also not static; temporal fluctuations in ocean circulation dynamics can alter connectivity over relatively short timescales [63]. Biophysical dispersal models, which are themselves IBMs that couple ocean circulation models with particle-tracking simulations [64], have enabled considerable progress in quantifying marine connectivity [65]. By tracking individual propagules through time, simulations reflect the strength and direction of dispersal according to circulation systems (figure 1b). Biophysical estimates of potential connectivity can then be used to evaluate the likelihood that vulnerable populations will receive stress-adapted migrants [66].

The output of biophysical dispersal models can be incorporated directly in eco-evolutionary IBMs as user-defined migration parameters (figure 1c). In the IBM developed by Matz *et al.* [34], migration probabilities between reefs were defined based on a long-term average forward transition matrix computed from a biophysical model of oceanographic transport over two decades. This approach involves a transformation of single-generation direct dispersal from one site to another such that the transition matrix incorporates dispersal from intermediate sites across multiple generations, thereby integrating migration probabilities across time [67]. Alternatively, connectivity matrices could be updated from one time step to the next to simulate changes in dispersal probabilities (figure 2c). While not an investigation into the potential for adaptation to climate change, this was the approach used by Moody *et al.* [30] (electronic supplementary material, S1), in

which dispersal probabilities from a biophysical dispersal model were updated weekly in eco-evolutionary IBMs exploring the effects of immigration on predator-driven local adaptation in the goby (*Sicyopterus stimpsoni*) in Hawaii.

Both [33,34] used biophysical dispersal models, either to lend support to migration rates inferred from demographic modelling [33] or to define migration parameters directly in eco-evolutionary IBMs of coral adaptation to climate change [34]. These models demonstrated that immigration could promote long-term metapopulation persistence under warming scenarios by redistributing adaptive genetic variation, and that influx of warm-adapted recruits did not negatively impact the capacity for coral populations to adapt to their local thermal environment. At a broad spatial scale, disconnected coral populations were initially resilient during warming, due to standing genetic variation that was already present locally, but ultimately showed rapid declines without recruits from warmer locations [34]. Using this approach, populations that did not receive immigrants from warm-adapted populations could be identified and prioritized for management interventions.

Bay *et al.* [32] highlight a promising application of IBMs to test conservation interventions like assisted gene flow (AGF; or assisted migration). AGF has been proposed as a management tool for mitigating negative effects of climate change by accelerating adaptive evolution in vulnerable populations [68]. The use of AGF to enhance coral reef resilience has been proposed [69,70], but the extent to which it can facilitate rapid adaptation is difficult to predict. Following from previous empirical work that identified loci associated with heat resistance in *A. hyacinthus* [39], IBMs in [32] showed that transplanting individuals from heat-tolerant populations

accelerated adaptation and facilitated persistence. However, accounting for transplant and juvenile mortality suggested that costs could be significant, especially for larger populations. Moreover, introducing individuals with only a few heat-tolerant alleles did not impact the speed of adaptation, indicating the need to ensure that populations targeted for transplantation are genetically preadapted to future conditions. This is an important concern, and benefits and risks must be carefully weighed to avoid wasted (or deleterious) effort [68].

(a) Opportunities for development

While the studies that we reviewed demonstrate the promise of eco-evolutionary IBMs that incorporate realistic estimates of migration, they also call attention to the potential for this approach to enable further exploration of the impact of gene flow on adaptation to climate change. An important concern in AGF efforts is the possibility of introducing alleles that are maladaptive in the new environment [31]. This was not addressed directly in simulations by Bay *et al.* [32], but they do indicate that future studies should consider this potential risk in predictions. It might be particularly important to model scenarios that include environmental variables other than temperature, as AGF to move warm-adapted alleles may introduce alleles that are incompatible with other conditions in the recipient population.

Climate change is also likely to alter dispersal pathways for many species via impacts on circulation dynamics [71,72]. Moreover, changes in local conditions such as temperature, pH and salinity can affect larval development and survival [73], release timing [74], swimming behaviour [75] and responses to settlement cues [76], all of which can impact the scale and degree of connectivity. Projections of climate-driven changes in marine connectivity have not yet been integrated into eco-evolutionary IBMs, and whether alterations to connectivity are likely to impact adaptive potential is an important open question. However, biophysical dispersal models have been used to generate predictions of future marine connectivity [77–79]. For example, models of larval dispersal for the dusky grouper (*Epinephelus marginatus*) using past and projected current velocities and hypothesized temperature-dependent shifts in larval growth and reproductive timing predicted increased overall metapopulation connectivity in the future [77]. Predictive biophysical larval dispersal models provide an opportunity to integrate estimates of future connectivity into eco-evolutionary IBMs by updating connectivity parameters (figure 1c) along with climate shifts. Going forward, this will require development of downscaled forecasts of circulation dynamics across geographical regions (e.g. [80,81]), demanding collaborations between physical oceanographers and marine evolutionary ecologists.

5. Multiple stressors

The studies we identified demonstrate the use of IBMs to predict the potential for populations to adapt at a pace that promotes persistence in the face of climate change, but none are complete explorations of the biological systems they focus on, nor do they claim to be. As stated in [34] ‘...our model is an abstraction designed for one purpose only: to reveal variation in adaptive potential among reefs and identify its environmental predictors. It is not a model of reality, because it assumes that adaptive potential is the only factor relevant

for reef persistence’. Existing eco-evolutionary IBMs of marine systems have largely focused on thermal changes [32–34]. Other factors including changes in abundance and identity of predators, pathogens, competitors, and symbionts [82–85], exploitation [86] and other sources of mortality or reduced reproductive success such as ocean acidification [87] are expected to exacerbate effects of ocean warming. For example, ecological models of coral communities show that combined effects of ocean acidification on growth and competitive interactions hinder recovery following multiple disturbances (crown-of-thorns outbreak, severe storms), but if only growth is affected, community recovery is possible [88]. In turn, interactive effects of multiple stressors and responses can affect the potential for adaptation to climate change [9,10]. While fully capturing biological reality in any model is not possible, IBMs can generate expectations regarding the contribution of multiple challenges to adaptive potential.

(a) An example using eco-evolutionary IBMs

We illustrate this approach by taking advantage of the detailed spatially and genetically explicit non-Wright–Fisher (non-WF) modelling framework, implemented in SLiM3 [25] provided by Matz *et al.* [34] to simulate populations of a hypothetical marine species distributed along latitudinal and thermal gradients under three eco-evolutionary scenarios: the first represents climate warming, while the second and third scenarios incorporate additional stressors that are hypothesized to result in severe reductions in population size (e.g. overexploitation or acidification) and reduced connectivity (e.g. physical barrier or loss of critical stepping-stone populations). Scenario 1 (figure 2a) incorporates a projection of extreme ocean warming (RCP 8.5), which should have the strongest effect on persistence over relatively short timescales [89]. To this warming scenario, we layered effects of a population bottleneck in the northern part of the range that precedes the onset of warming (scenario 2, figure 2b) and a break in connectivity between southern populations, a source of adaptive alleles and northern populations, followed by the bottleneck and warming as in previous scenarios (scenario 3, figure 2c). Full model details are provided in electronic supplementary material, S2.

Under warming only, southern populations show reduced fitness 10 years after warming begins, and many are lost after 20 years following the onset of warming (figure 2a). Over time, there is a linear pattern of extinction from south to north, with northernmost populations persisting after 50 years post-warming (figure 2a; electronic supplementary material, S3 and video S1). Scenario 2 revealed that an additional stressor, a reduction in population size immediately prior to the onset of warming, hastens the rate of population decline. Although many northern populations are able to recover during the warming period (figure 2b), more northern populations are lost compared to scenario 1 by 50 years (figure 2b; electronic supplementary material, S3 and video S2). Scenario 3 shows that breaking connectivity between the northern and southern populations, which in this case occurs prior to the onset of warming, further hastens the loss of the northern populations: more than half of the populations are lost within 20 years of the start of warming (figure 2c; electronic supplementary material, S3 and video S3). Adaptive potential of northern populations was clearly dependent on gene flow from southern populations, which presumably harboured alleles conferring higher fitness in warmer temperatures.

These simulations are not meant to represent any real marine system, but to highlight the flexibility of the IBM framework for testing hypotheses regarding the effects of multiple factors on the capacity for adaptation and persistence in the face of warming. Incorporating effects of multiple biological stressors in a realistic manner is challenging, not only because it will increase the complexity of the model, but also because of limits to biological knowledge. While further experimental work will be needed to accurately parametrize impacts of multiple challenges, IBMs offer a solution for incorporating complexity and provide a convenient approach for testing hypotheses. The latest expansions to the SLiM3 framework, including non-WF models [25], are particularly useful as they allow for overlapping generations and complex age structures with more flexibility in reproduction, population regulation and migration (among other processes). Furthermore, it is now possible to simulate spatial interactions and incorporate multiple spatial maps of different environmental variables, paving the way for explicit integration of multiple environmental effects. Together with genetically explicit approaches, it should be possible to consider potential constraints introduced by multiple selective pressures that may lead to fitness trade-offs [90]. These developments provide an opportunity for users to explore the power of IBMs to model increasingly complex eco-evolutionary scenarios, including impacts of multiple stressors, on the potential for adaptation in changing seas.

6. Conclusion

Predicting the potential for marine species to adapt to rapidly changing environments is an important albeit challenging goal, given the many factors contributing to adaptation and the multidimensional effects of the various threats facing marine populations. While models may fall short of reality, eco-evolutionary IBMs provide an ideal framework for identifying key variables that may influence adaptation, assessing the sensitivity of model outcomes to various scenarios and testing the efficacy of human interventions (table 2). The relatively small number of studies retrieved in our literature survey suggests that eco-evolutionary IBMs are only now emerging as tools to predict adaptation to climate change in marine systems. Nevertheless, we expect wider adoption given the increasing computational efficiency and accessibility of modelling tools. The taxonomic scope of the literature is also relatively limited, with most studies focusing on corals or fishes. However, this

type of approach may be especially helpful in systems for which high-resolution data needed for parametrizing models are not yet available. Reasonable ranges can be tested to determine the sensitivity of outcomes to specific parameters and efforts can be focused on collecting critical data. The studies we identified (table 1; electronic supplementary material, S1 and table S1) as well as our simple exemplar models provide resources for those wishing to apply eco-evolutionary IBMs to investigate adaptation to changing seas in diverse systems.

Data accessibility. The original data from the biophysical model used in figure 1*b,c* were previously published in Xue *et al.* [38]. The dataset from the biophysical model that was used in this paper and the code to compute and plot dispersal trajectories are available at https://github.com/amandaxuereb/LarvalTrajectories_IBMpaper. Connectivity matrices used to generate figure 1*c* and surface temperature rasters for use in the SLiM models are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j6q573nfd> [91]. All scripts and data used to perform SLiM simulations and results files are available at https://github.com/QuentinRougemont/marine_IBM_paper.

Authors' contributions. All authors contributed to the conceptualization, execution and revision of the manuscript. A.X. coordinated the study, drafted and edited the manuscript, and created the figures. M.P.-R. and A.X. performed the literature search; M.P.-R. generated table 1 and electronic supplementary material, table S1, and wrote the description of the literature search findings. M.P.-R. and P.T. helped draft and critically revised the manuscript. Q.R. performed the simulations, with input from A.X. and P.T., drafted electronic supplementary material, ESM2 (simulation methods), created the videos (electronic supplementary material, ESM3) and revised the manuscript. H.X. provided biophysical model output from the Gulf of Maine and revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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