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Editorial

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Evolution in changing seas

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Rapid environmental change continues to have alarming consequences for the world's oceans, including shifts in the distribution and phenology of species, the nature and strength of species interactions, and the alteration of ecosystems and provision of their services [1–3]. Threats to biodiversity from overharvesting, climate change, invasion, habitat degradation, disease and their combined effect are amplifying [4,5], suggesting that local and global extinctions will soon follow [6]. Despite the growing body of research documenting the effects of environmental change on marine species, communities and ecosystems, the field has yet to develop robust predictions of how marine species and ecosystems will ultimately respond, persist or recover under these threats [7,8]. Because such predictions require a basic understanding of how organisms have adapted to their current environments—and how such adaptation may shape the capacity of future generations to respond—any successful predictive framework must integrate the principles of evolutionary biology. As famously noted in 1973 by Theodosius Dobzhansky, 'Nothing in biology makes sense except in the light of evolution.'

While the study of the interaction between physical, chemical and biological processes has yielded considerable insight into the ecology of marine and other systems, evolutionary thinking has not been historically well integrated within the ocean sciences. In marine systems, oceanographic forcing is a key factor driving evolutionary processes. Dispersal (gen flow), random mortality (drift) and non-random mortality (selection) all occur for species within oceanographic settings, which results in strong coupling between physical and evolutionary processes in the sea [9,10]. At the same time, there is potentially strong decoupling between the larval environment (and origin) and adult environment, especially for sessile organisms with pelagic larvae [11]. Marine species are also often characterized by large effective population sizes, high fecundity and potential for long-distance dispersal of gametes or larvae. Despite this high dispersal capacity, many marine species exhibit local adaptation on spatial scales well below the dispersal distance (microgeographic adaptation) [8,12,13]. While an understanding of evolutionary processes is key to predicting responses to climate change, considering these aspects of marine systems can also give new insights into evolutionary processes. This Special Feature highlights research at the intersection of evolutionary processes and marine science that aims to advance knowledge in both fields.

Both adaptation and phenotypic plasticity can facilitate population persistence in a changing environment [11,14]. A widespread notion is that populations experiencing increased climate variability (e.g. fluctuations) will evolve increased plasticity, thereby making them less vulnerable to environmental change. This idea, known as the 'climate variability hypothesis', arose from a prediction in macroecology that species from thermally variable environments should tend to have broader thermal niches [15]. This idea also forms the basis of indexes of population vulnerability based on climate novelty [16,17], which are based on the amplitude of historical climate fluctuations experienced by a population.

Two studies in this Special Feature challenge the widespread notion that increased climate variability also increases thermal tolerance and plasticity [18,19]. Bitter *et al*. reviewed theoretical predictions for the evolution of plasticity in fluctuating environments, and showed that it is the predictability

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(rather than the amplitude) of fluctuations that primarily drive the amount of phenotypic plasticity present in natural populations. They also showed that because most experimental studies in marine systems have manipulated the amplitude, and not the predictability, of fluctuations, effective tests of theory have rarely been conducted [19]. They proposed an experimental design that future studies can use to tease apart the effects of the amplitude, predictability and novelty of climate fluctuations on population fitness and persistence [19]. In another study, Barley *et al*. conducted a meta-analysis of within-species variation in thermal plasticity, but did not find support for the climate variability hypothesis [18]. Instead, their analysis showed that populations with greater thermal tolerance had reduced plasticity, which was evidence for trade-offs between thermal tolerance and thermal plasticity [18].

Trade-offs can also manifest across the life cycle and across environmental gradients. Two studies in this Special Feature provide different perspectives on trade-offs. Albecker *et al*. reviewed how trade-offs manifest across complex life cycles, and showed that the field still has a poor understanding of whether trade-offs across the life cycle will constrain or promote adaptation in response to rapidly changing environments [20]. They showed how genomic data can be used to provide new insights into life cycle trade-offs, and how within-generation selection experiments can be designed to test whether climate change reshapes fitness trade-offs among life stages [20]. On the other hand, trade-offs can also manifest across environmental gradients on short spatial scales, whereby organisms seeking refuge from a major stressor will be exposed to another stressor [21]. In another study, Blakeslee *et al*. showed how this conundrum is faced by mud-crabs in estuaries, whereby the selective pressure from an invading castrating parasite occurs at high salinity sites, but refuge from the parasite at low salinity sites imposes osmotic stress [22]. Blakeslee *et al*. found evidence consistent with the hypothesis that standing genetic variation for salinity tolerance allowed mud crabs to find refuge from the body-snatching parasites at low salinity sites, thus reshaping the ecological landscape of the species [22].

The evolutionary capacity of organisms to evolve in response to novel environments arises from both phenotypic plasticity and standing genetic variation, both of which can follow a genetic model of inheritance [23,24]. Plasticity can also be induced in parents and then inherited and expressed by offspring; such transgenerational plasticity can follow an epigenetic model of inheritance [25]. Griffiths *et al*. teased apart the roles of standing genetic variation and transgenerational plasticity in low salinity tolerance of the Eastern oysters in the Gulf of Mexico, which is predicted to experience declining salinities under climate change. Low salinity conditions resulted in slower growth and reduced body size at metamorphosis, which was associated with mortality at later stages [26]. While they did not find evidence of strong transgenerational plasticity, they did find high heritability for body size under low salinity conditions, suggesting that there is ample genetic variation for this trait to evolve in response to declining salinity in the future [26].

Standing genetic variation can also manifest across metapopulations, with among-population differences in the capacity to withstand stress. For ectothermic species distributed across broad temperature gradients, metabolic theory predicts that populations residing in warm locations will have higher rates of growth compared to those residing in cool habitats because warming increases the rate of metabolic processes [27]. Villeneuve tested this prediction with data characterizing the performance of a marine snail across latitudinal thermal gradients in North America [28]. Using common garden experiments, they found that, contrary to theory, northern (cooler) populations had higher thermal optima and higher maximum growth rates than southern (warmer) populations, despite experiencing overall cooler temperatures [28]. Although inconsistent with metabolic theory, these complex patterns of thermal performance curves are consistent with a pattern of ‘latitudinal compensation’, in which northern populations exhibit elevated growth rates compared to southern populations [29]. Such findings are important for more accurate predictions for how populations within species will respond to climate change.

Understanding the interaction of gene flow, selection and genetic drift is also important for understanding metapopulation responses to climate change. How these evolutionary processes unfold is particularly important—but rarely elucidated—at range margins, where edge populations play a critical role in enabling species to adapt to changing environments [30]. Clark *et al*. [31] showed that although the northern range margin of a clownfish species experiences strong genetic drift and has reduced genetic diversity, their genomes also showed evidence that is consistent with thermal adaptation at the range margin. These results illustrated how range edge populations can become locally adapted, despite the potential for both strong genetic drift at the range edge and moderate gene flow from the core populations [31].

Ultimately, the integration of oceanographic and eco-evolutionary frameworks is urgently needed to foster robust predictions of how organisms will respond to climate change, and to inform effective management strategies. Xuereb *et al*. reviewed the use of eco-evolutionary individual-based models to achieve these goals, and highlighted opportunities for the development of models that advance our understanding of how oceanographic processes, genetic architecture, non-genetic inheritance, demography and multiple stressors interact to promote or constrain adaptation to environmental change [32]. Importantly, Xuereb *et al*. also provided a simulation case study that illustrates how to incorporate patterns of connectivity based on oceanographic models into an eco-evolutionary model to predict the distribution of a species under different climate change scenarios [32]. Because population connectivity can strongly influence the sources and sinks of genetic variation that serve as the fuel of evolutionary change, it is essential that we better understand its role in shaping adaptation across multiple spatial and temporal scales. This will inform the vital role that connectivity plays in management and conservation [33–35].

In the absence of drastic, cooperative change in emissions, oceans, seas and coasts are likely to undergo abiotic shifts that may generate novel (no analogue) ocean chemistries and temperature regimes [17]. Research at the intersection of oceanographic, ecological and evolutionary processes is critical to advance our knowledge of how biodiversity will ultimately respond to this novelty. The research presented in this special issue advances our knowledge not only by challenging previously held ideas, but also by generating new methods that can be applied to diverse systems and taxa, offering new insights via synthesis, and stimulating research questions to guide future research. Such advances will aid in efforts to preserve marine environments and the biodiversity they sustain.

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