

Methods for Measuring Evolutionary Potential in Marine Biota

Abstract

Climate change has negatively affected the world's oceans through increased water temperatures and acidification, and marine biota have exhibited strongly negative reactions to these changes. However, many preliminary studies have failed to account for marine biota's potential to adapt to future environmental conditions. This paper reviews the various methods that exist for measuring evolutionary potential in marine species, including quantitative genetics, molecular genomics, and experimental evolution. The strengths and limitations of each method are outlined, and notable examples of each method from the literature are reviewed. Finally, the results of existing studies are summarized, and suggestions are made for future improvements to studies of evolutionary potential in marine organisms.

Introduction

Global climate change is unequivocally altering the world's oceans through warmer water temperatures and increased acidification (IPCC, 2014). Acting in tandem, these abiotic environmental changes have already begun to impact marine biota. Fluctuations in temperature have caused poleward range shifts in many species, mismatches in reproductive events and food availability, migratory failures, and complete population collapses (Portner and Farrell, 2008). Ocean acidification, in turn, has caused decreases in survival, calcification, growth, development, and abundance across a wide variety of taxa (Kroeker et al., 2013). Faced with these troublesome results, it is natural to wonder how marine organisms will survive future climate change. Indeed, the last decade saw an explosion of

studies investigating the impacts of climate change on marine ecosystems (Brown et al., 2011; Wernberg et al., 2012). However, while these studies have provided invaluable information about climate change impacts, filling a crucial knowledge gap, they still suffer from a number of weaknesses. For instance, in the papers published between 2000 and 2009 that focused on the effects of climate change on marine ecosystems, 65% of them only tested a single climate change factor, and 58% were restricted to a single species (Wernberg et al., 2012). Given the complexity of the marine food web and the potentially multiplicative effect of many environmental stressors, these studies suffer from unrealistic simplicity. Similarly, only 11% of these studies included a field component, indicating again that these experiments fail to capture the many nuances of the environment (Wernberg et al., 2012).

Still, perhaps the most glaring error in these early works was their failure to account for adaptation by marine organisms. The majority of these pioneering studies focused on short-term, acute studies of adverse conditions, measuring changes in growth and behavior after only a short acclimation period to novel conditions (Gibson et al., 2011). Such studies may overestimate instances of mortality by ignoring the potential of marine organisms to adapt (Pandolfi et al., 2011). In response, a growing number of studies have begun to investigate responses to climate change through an evolutionary lens.

Although the climate is changing at an unprecedented rate, preliminary studies indicate that microevolution can occur at rates that are relevant to current and projected climate change (Skelly et al., 2007). For instance, rapid evolutionary

transitions have been documented within only a few generations, even in long-lived species, disproving the argument that evolution only occurs at prohibitively long timescales (Kinnison and Hendry, 2001; Shaw and Etterson, 2012). Still, the ultimate goal of this research is not only to determine if microevolution is possible, but if populations will be able to persist under future conditions. Therefore, it is necessary to include other relevant factors such as demographic parameters. For instance, smaller populations have a decreased potential for adaptation, as they have less genetic variation and are placed under further stress by genetic problems such as inbreeding (Willi et al., 2006). Therefore, the most rigorous studies should include both demographic and genetic information to determine if populations will persist (Hoffman and Sgro, 2011; Gonzales et al., 2013).

This paper will provide a review of the current literature that investigates adaptations to climate change in the marine ecosystem. It begins with a brief discussion of phenotypic plasticity versus true microevolution, and the common pitfalls of studies that confound the two. Next, it will outline the primary methods used to measure evolutionary potential, and the strengths and limitations of each method. Finally, it will identify key gaps in current knowledge, and provide relevant suggestions for future work.

Adaptation or Acclimation?

As mentioned previously, a number of studies have investigated the responses of organisms to climate change, concluding that microevolution has occurred (Gienapp et al., 2008). However, most of these studies fail to provide genetic evidence of this

change, and rely primarily on phenotypic data when making their claims; an analysis by Gienapp et al. (2008) revealed that only 3 of 105 studies on climate-mediated responses gave genetic evidence for their results. Consequently, these studies are unable to distinguish between true microevolution and phenotypic plasticity. Evolution occurs when selection acts on a trait that has both variation and heritability, resulting in a change in allelic frequency in a population.

Phenotypic plasticity, on the other hand, is the ability of a single genotype to produce multiple different phenotypes in response to environmental changes.

Understanding the difference between microevolution and phenotypic plasticity is key in climatic studies, as they provide different services to adapting organisms.

Phenotypic plasticity can be broken down into three types: reversible, developmental, and transgenerational (Sunday et al., 2013). Reversible phenotypic plasticity occurs when an organism modifies its physiology, morphology, or behavior on a scale of weeks to months (Angilletta, 2009). For instance, temperate fish species, which experience high seasonal fluctuations in temperature, show plastic adaptations to their muscles in order to optimize swimming performance at different temperatures (Johnston, 1993).

Developmental phenotypic plasticity occurs during ontogeny; early exposure to a new environment enhances an organism's performance in that environment later in life (Scott and Johnston, 2012). Studies on developmental phenotypic plasticity are less common than those of reversible plasticity, as they must follow an organism from birth to much later in its development. Still, some have been successful, demonstrating that fish reared at 3° C higher than average had a lower resting

oxygen consumption compared to fish reared at average temperatures and later exposed to higher temperatures (Donelson et al., 2011; Grenchik et al., 2013). These studies indicate that coral reef fish experience developmental acclimation that may help them cope with future climate change.

Phenotypic plasticity can also extend beyond the life of an individual organism, in the form of nongenetic information inherited from its predecessors (Burgess and Marshall, 2011). Parents can transmit nutritional, somatic, cytoplasmic or epigenetic material to the next generation, and so modify the offspring's phenotype without a genetic change (Bonduriansky et al., 2012). This transgenerational information can have a positive or negative effect on offspring. In terms of negative effects, one study found that female damselfish with higher stress levels produced larvae of lower quality (McCormick, 1998). However, when considering climate effects, many studies have found a positive impact on offspring when parents are exposed to adverse conditions. One such study showed that exposure of parents to high levels of carbon dioxide mitigated a negative response of juvenile offspring to increased CO₂ (Allan et al., 2014). While control juveniles demonstrated a decreased escape response at high CO₂, which could affect prey's ability to evade predators, juveniles with parents who experienced high CO₂ had enhanced performance in comparison (Allan et al., 2014). In another study focused on temperature and body size, sticklebacks were reared at high and low temperatures, then their offspring were exposed to high and low temperatures. In this study, not only did offspring demonstrate larger body size when raised at the temperature of their parents, but the benefit of this transgenerational plasticity was stronger and

persisted longer in the high temperature treatment, indicating that transgenerational effects will be more important under future warm climate scenarios (Shama et al., 2014).

Clearly, phenotypic plasticity can play an important role in helping marine organisms to adapt to new environmental conditions. Still, it is important to distinguish between phenotypic plasticity and microevolution, as each have unique benefits and limitations. A boon of phenotypic plasticity is in its speed, occurring at timescales of a single generation, or even weeks within an organism's life. However, plastic responses are often limited; in comparison with genetic changes, plastic responses cannot produce as extreme phenotypes (Gienapp et al., 2008). Thus, a population that is forced to rely solely on phenotypic plasticity when responding to a changing environment may not be able to adapt past a certain threshold, demonstrating that acclimation cannot always provide a long-term solution. Indeed, plasticity is often discussed in terms of its ability to provide temporary relief to populations in changing conditions. Plastic responses can buffer populations from adverse environmental conditions and allow genetic adaptations to "catch up" (Chevin et al., 2010). Conversely, it has also been theorized that plasticity might slow genetic change by improving population fitness, and thus reducing selection, without actually changing allelic frequencies (Sunday et al., 2013). Finally, acclimation may also occur at a cost to an organism. For instance, in the study on water temperature and oxygen consumption, while the fish reared in warm water experienced acclimation to summer temperatures, they were also smaller and in poorer condition than fish reared at present-day temperatures (Donelson et al.,

2014). Thus, reduced oxygen consumption came at the cost of size and body condition. Overall, phenotypic plasticity and microevolution can both contribute to climate adaptation strategies of marine organisms, but it is still important to differentiate the two as they play very different roles in affecting evolutionary potential.

Measuring Evolutionary Potential

To forecast the future for marine organisms under climate change, it is necessary to look back to the basic principles of selection set down by Darwin. For natural selection to act on a trait, the trait must have variation that is heritable (Darwin, 1859). It is this existing, or standing, genetic variation in a population that allows for adaptation to occur. New mutations are also possible, but given the unparalleled rates of climate change predicted in the near future, it is generally accepted that standing genetic variation will be the primary fuel for adaptation to climate change (Hendry et al., 2011). Thus, one of the best proxies for evolutionary potential is standing genetic variation in traits that respond to changing environmental conditions (Munday et al., 2013). There are a number of methods for measuring this standing genetic variation, each with their own costs and benefits, which are reviewed below.

Quantitative Genetics

Classic genetic theory dictates that phenotypic variance is controlled by both genetic and environmental components (Lynch and Walsh, 1998). Quantitative genetics compares relatives with known genetic relatedness to separate the genetic and environmental components of a trait's phenotypic variance (Lynch and Walsh, 1998). A major benefit of this method is that fitness traits can be directly examined, without any knowledge of the specific genes involved in the process (Sunday et al., 2013). Furthermore, useful results can be obtained through a single generation, meaning that studies do not have to be especially time-consuming (Munday et al., 2013).

However, limitations to quantitative methods also exist. Most studies require broadcast spawning in specimens, so as to more easily create multiple crosses, limiting possible study species to fish, mollusks, and crustaceans (Munday et al., 2013). Furthermore, most methods require populations to be raised in captivity, posing limits to the size of feasible study species (Munday et al., 2013). However, in recent years implementation in natural populations has been proposed and successfully, though sparingly, employed in marine species (e.g. Domingos et al., 2013). Additionally, quantitative genetic studies require at least 20 sires to generate useful results, potentially raising the total number of individuals involved up to the thousands, which can quickly become burdensome and costly to experimenters (Conner and Harti, 2004).

Beyond these logistical issues, quantitative genetic methods also have an inherent tradeoff; although they are able to predict evolutionary potential without specific

genetic information, they also cannot provide information about the underlying mechanisms of adaptation as molecular genetic methods can (Munday et al., 2013). Finally, while quantitative methods are ideal for targeting specific traits, the overarching purpose of estimating evolutionary potential is to see whether populations will persist in the future, which requires an estimate of total fitness. However, it is extremely difficult to target all of the traits that contribute to overall fitness, and so quantitative genetic studies may struggle to completely encapsulate evolutionary potential (Munday et al., 2013). Nevertheless, quantitative methods are invaluable for examining evolutionary potential in fitness-related traits without specific genetic information.

Under the umbrella of quantitative genetics, a number of different methods exist. The simplest method employs clonal organisms, which in the marine environment include taxa like seaweeds, corals, bryozoans, and sponges (Monroe and Poore, 2005). These species can be easily replicated by fragmentation, resulting in a series of clones that are assumed to differ only in environmental, not genetic, variation (Sunday et al., 2013). Thus, by comparing variance within and between clones, the broad sense heritability H^2 can be measured (Lynch and Walsh, 1998). This method unfortunately trades simplicity for precision, as broad sense heritability cannot distinguish true genetic change from phenotypic plasticity, and therefore can easily overestimate standing genetic variance on a trait (Sunday et al., 2013).

Still, clonal studies have been used successfully to measure broad sense heritability and standing genetic variation in some species. For instance, in one study, multiple clonal lines of the bryozoan *Celleporella hyalina* were exposed to future temperature

and CO₂ conditions (Pistevos et al., 2011). The results revealed differential responses to these novel conditions between clonal lines, suggesting that the species has the standing genetic variation to adapt to climate change. A similar study examined the response of clonal lines of eelgrass *Zostera marina* to increases in temperature (Ehlers et al., 2008). They found evidence for differential performance between clones and a positive effect of genotypic diversity on eelgrass density, again pointing to the importance of genetic diversity in adapting to adverse conditions (Ehlers et al., 2008). Though these studies are limited in the inferences they can draw, they still provide useful information on genetic diversity within clonal organisms.

Another common quantitative genetic method is known as a diallel or factorial breeding design. A number of males and females are crossbred, with every male mating with every female (Munday et al., 2013). Using information from both parents and the offspring, this method can extend beyond broad sense heritability to capture additive genetic variance h^2 , or the phenotypic variance that is due to additive, heritable genetic variation (Wilson et al., 2010). This method is particularly suited to broadcast spawning species, as the eggs and sperm can be easily separated for crossbreeding (Sunday et al., 2013).

For instance, Foo et al. (2012) examined the sea urchin *Centrostephanus rodgersii* under increased temperature and decrease pH as projected under future conditions. They found evidence of heritable variation in thermal and pH tolerance, indicating that the species will be able to adapt under future climate change (Foo et al., 2012). Another study found heritable variation in thermal sensitivity in the intertidal

microalga, *Hormosira banksii*, indicating a potential for future adaptation (Clark et al., 2013). However, a similar study on a broadly distributed copepod found little evidence of additive genetic variation for increased thermal tolerance, suggesting little evolutionary potential in the species' future (Kelly et al., 2012). Overall, it seems that responses to temperature and pH are highly species-dependent, and so further work is needed to examine responses in other species.

A final quantitative genetic method that is gaining traction in the marine literature is known as the animal model. Similar to a diallel breeding design, it relies on analysis of organisms of known relatedness to partition the environmental and genetic components of variation. However, the animal model is able to accommodate complex, multigenerational relationships, conferring a number of key advantages to this method (Kruuk, 2004). The animal model is so named because it focuses on variation at the level of the individual animal, as opposed to evaluating sires in terms of their offspring (Kruuk, 2004). An individual's phenotype y is written as:

$$y = \mu + a + e$$

where μ is the population mean, a is the additive genetic component, and e is a random residual error (Kruuk, 2004). The beauty in the simplicity of this model is that additional confounding effects can be easily accommodated by incorporating extra random effects into the model. For instance, local environmental conditions may affect phenotype expression, such that individuals raised in the same environmental conditions have similar phenotypes. Thus, if siblings tend to be raised in the same environment, they will have greater covariance than is predicted by solely their genetic relatedness, resulting in conflation of estimates of heritability

(Kruuk, 2004). The animal model solves this problem by incorporating common environment as an extra random effect, resulting in lower, and more realistic values for heritability (Kruuk, 2004). Similarly, maternal effects, or transgenerational phenotypic plasticity from an individual's mother, can create covariance between siblings that is not genetic in nature. This too can be incorporated into the animal model with an extra random effect (Kruuk, 2004). Because the animal model is able to partition environmental and plastic responses from genetic effects, its estimates of heritability are often lower than those predicted using other methods, though these estimates are also likely more accurate (Kruuk, 2004).

The animal model is also useful in the breadth of information it can receive. It is not constrained by assumptions of no assortative mating, inbreeding, or selection, which are realities in natural populations (Kruuk, 2004). As a result, proposals have been made to use the animal model on natural populations (Wilson et al., 2010).

While such studies have been rare, initial results are promising (e.g. Domingos et al., 2013) and such studies will likely continue to grow in numbers. The animal model is also valued because it can incorporate data on multiple phenotypic traits (Kruuk, 2004). Since natural selection usually acts on many traits simultaneously, this brings experimental methods closer to real-world dynamics. A final benefit of the animal method is that it can be applied to many more species than other quantitative methods, as it does not require experimenter manipulation of eggs and sperm. However, when crosses are not created artificially, the parentage of offspring is not always obvious, and so molecular methods must be incorporated to build pedigrees (Kruuk, 2004).

The animal model requires high computational intensity, which may explain its limited use in marine climate studies (Kruuk, 2004). However, it has allowed strong inferences to be drawn in cases where it has been used. For instance, in a study on thermal effect on stickleback body size, an animal model revealed the importance of maternal effects in different climate regimes (Shama et al., 2014). When compared across high and low temperatures, the model also highlighted the fact that maternal effects persisted for a longer duration of an individual's lifetime at high temperatures, indicating that maternal effects will be more important in future warm climates (Shama et al., 2014). Another study on brown trout analyzed a number of early life-history traits for their variance in response to temperature, and found evidence for additive genetic variance in many of the traits, indicating future evolutionary potential (Jensen et al., 2008). This study is noteworthy for taking advantage of the animal model's ability to analyze multiple traits in a population. While these studies serve as useful examples of the animal model in action, the method is still underused and offers much potential. Future work should move towards including more complex systems, and even analyzing natural systems.

Molecular Genetics

Recent advances in molecular genomics techniques have created new opportunities for investigating evolutionary potential in marine organisms. Through methods like transcriptomics and DNA sequencing, scientists have been able to identify standing genetic variation at multiple loci that are responsive to climate change (Sunday et al., 2013). Beyond identifying genetic variation, scientists have also documented

genes exhibiting different activation pattern under different environmental conditions, and identified the molecular pathways that underlie trait expression (Munday et al., 2013). Molecular methods are particularly beneficial for use in large or long-lived species that could not undergo breeding experiments in the lab. It is also hoped that the results of molecular studies will reveal common genetic and physiological mechanisms that are conserved across species, allowing for extrapolation of results without needing to analyze genome-level data in all marine species (Munday et al., 2013).

However, molecular genetic methods suffer from a number of limitations. While they can elucidate genetic variation and differential allele expression, it can be difficult to link these changes to fitness-related phenotypes and demonstrate their heritability (Munday et al., 2013; Sunday et al., 2013). Thus, while they are useful for providing precise molecular and mechanical information, they do not always predict the heritability of polygenic traits (Munday et al., 2013). Another problem that has arisen in molecular genetics is a fairly limited selection of model organisms. Given the profound level of detail required for molecular genetic methods, it is simply not feasible to analyze all marine organisms in this way. Thus, scientists have relied on a small pool of model organisms that have been extensively studied for use in molecular genetics. While model organisms such as *S. purpuratus*, discussed below, have provided extensive information on genetic variation in climate-related traits, they very likely do not reflect the reaction of all marine organisms to climate change (Sunday et al., 2013). Model organisms are often share traits like small body size and high abundance, which make them easy to procure

and use in the lab, but these traits are not indicators of any particular ecological importance (Sunday et al., 2013). Therefore, scientists must proceed with caution before extrapolation results to other species. Recently, new advances in the field have allowed molecular genetic techniques to be used on non-model organisms, indicating that future studies will be able to avoid some of these problems (Arnold et al., 2012).

Still, model organisms have fueled a number of key studies in the field of molecular genetics. For instance, the sea urchin *Strongylocentrotus purpuratus* has been used extensively to monitor for genetic variation in responses to ocean acidification (Evans et al., 2013; Pespenti et al., 2013a; Pespenti et al., 2013b). In the year 2013 alone, three major studies on the subject were published. The first examined genetic responses of adult populations of *S. purpuratus* under realistic future carbon dioxide levels, detecting signatures of genetic change across hundreds of loci (Pespenti et al., 2013a). These changes were found in genes known to control biomineralization, lipid metabolism, and ion homeostasis, all of which contribute to skeletal building and pH regulation (Pespenti et al., 2013a). Thus, this study was able to demonstrate existing genetic diversity on traits important to coping with ocean acidification. More interestingly, all of these allelic shifts occurred without any noticeable changes in morphology or development in the sea urchins, indicating that populations can adapt to climate change with little outward response (Pespenti et al., 2013a).

A few months later, another study on *S. purpuratus* used transcriptomics to investigate the mechanisms underlying pH tolerance (Evans et al., 2013). The

results showed that *S. purpuratus* larvae exhibited differential gene expression between present-day and future acidification conditions, with a muted response in future acidification scenarios (Evans et al., 2013). From this result, the authors suggested that even if present-day populations of *S. purpuratus* are adapted to low-pH conditions, this resilience may not confer success in future conditions (Evans et al., 2013).

However, a second paper by Pepseni et al. (2013b) offered a more optimistic result. Building off of their earlier work, they were able to pinpoint seven candidate genes for response to ocean acidification in *S. purpuratus* (Pepseni et al., 2013b).

Furthermore, they noted that in these genes, the alleles coding for low-pH adaptation were found both in natural conditions and experimentally acidified conditions, indicating that natural and artificial selection favor the same alleles (Pepseni et al., 2013b). This universality in response, they concluded, suggests that the species has the genetic capacity to evolve rapidly under future ocean acidification. Overall, the works of Evans et al. and Pepseni et al. provide compelling, contemporary examples of molecular genetics at work.

Experimental Evolution

The previously discussed methods have relied on theoretical assumptions of evolutionary potential— primarily, that standing genetic variation can indicate future survival under climate change. However, experimental evolution takes a more practical approach; organisms are subjected to projected conditions and allowed to proceed through multiple, often hundreds, of generations. These future-

adapted organisms are then compared to control populations, and their responses are measured (Munday et al., 2013). Similar to experimental evolution is artificial selection, when experimenters choose individuals for subsequent generations based on their phenotypes (Fry, 2003). Though artificial selection is less useful for mimicking natural trends, it can reveal correlated responses to climate change that are nonintuitive (Munday et al., 2013). Furthermore, it can be used to test for evolutionary tradeoffs, or instances when adaptation in one trait reduces performance in another trait— recall the fish that acclimated their metabolic rates to high temperatures, but had smaller size and poorer body condition (Donelson et al., 2014). Together, experimental evolution and artificial selection are powerful tools for demonstrating evolutionary potential.

Of course, as with the other methods, there are drawbacks to experimental evolution. Logistically, the experiments can be lengthy and costly. In contrast to quantitative genetic methods that can examine a single generation, experimental evolution often needs to proceed through hundreds of generations to generate useful results. This not only makes such experiments time-consuming, but also limits the organisms that can be tested through experimental evolution; long-lived, large, or delicate species are not amenable to these studies, and so they often focus on species with short generation times, small body sizes, and easy rearing in the lab (Munday et al., 2013). Just as with model organisms in molecular genomics, these ideal laboratory species will not always represent the responses of all marine organisms, and results must be extrapolated carefully. An additional burden to experimental evolution studies is the requirement for large populations. To most

completely capture the full range of standing genetic diversity within a population, experiments must include a very large initial population (Fry, 2003).

Understandably, such studies could easily fail to capture all genetic diversity within a population, resulting in inaccurate estimations of evolutionary potential (Munday et al., 2013).

Moving away from logistical limitations, experimental evolution also falls short in other areas. If performed in isolation and not combined with other methods, experimental evolution cannot separate true genetic adaptation from phenotypic plasticity, a common problem in early climatic studies (Sunday et al., 2013).

Additionally, like quantitative genetic methods, experimental evolution experiences a tradeoff between knowledge of evolutionary potential and mechanistic information; though it can infer evolutionary potential without explicit knowledge of the specific genes involved, it also cannot identify molecular pathways that underlie adaptation to climate change (Munday et al., 2013).

Despite these limitations, experimental evolution studies have been used to demonstrate trends in adaptation in ideal lab species like phytoplankton (Collins et al., 2014). A recent review surveyed instances of experimental evolution in 22 species of phytoplankton, including diatoms, dinoflagellates, and coccolithophores, that were exposed to acidified conditions, and examined the results for overarching trends (Collins et al., 2014). The taxa that experienced a decline in fitness when first exposed to acidified conditions later demonstrated adaptive evolution (Collins et al., 2014). This was primarily observed in coccolithophores, which initially experienced depressed growth rates, but eventually were able to partially

compensate by restoring calcification over several hundred generations of selection (Lohbeck et al., 2012; Benner et al., 2013). These results indicate that, given enough time, adaptation can mitigate or completely reverse the negative effects of acidification in coccolithophores (Benner et al., 2013). Conversely, in other taxa like diatoms and dinoflagellates, no negative response to acidification was observed; instead, their growth rates either remained constant or increased (Collins et al., 2014). Consequently, these taxa did not display signs of adaptation to increased acidity (Collins et al., 2014). The results of these studies are encouraging, demonstrating that many populations have the potential to adapt to future environmental conditions.

Conclusions and Future Work

The reviewed methods represent a number of modes for measuring evolutionary potential, each with their own strengths. Quantitative genetic methods, including clonal experiments, diallel breeding designs, and animal models, can reveal trends in the heritability of fitness-related traits without specific knowledge of the exact genes involved. Molecular genomics, on the other hand, can identify the specific loci involved in climate-related traits, the molecular pathways that underlie expression of those traits, and differential gene expression under different environmental conditions. Finally, experimental evolution puts theory to the test, and can document actual evolutionary responses to climate change. Ideally, future work will bring together these methods, allowing for deeper knowledge of the processes controlling climatic adaptations (Munday et al., 2013).

From the studies reviewed, we can see that many marine species exhibit the potential for future adaptation and acclimation to climate change. Many studies found evidence for both phenotypic plasticity and genetic adaptation to climate change, highlighting the importance of the buffering capacity of phenotypic plasticity. Within genetic adaptations, most studies found some standing genetic variation in climate-related traits, suggesting that populations have the potential to adapt to future warm climates. Similarly, the results of experimental evolution studies were promising, demonstrating in many species that long-term adaptation to adverse conditions was possible.

Still, further research is needed to more accurately predict if marine organisms will survive future climate change. One important shift needed in the future is towards more representative study species. As previously discussed, many study species are selected for their ease of manipulation in captivity. However, these species are not necessarily ecologically relevant, nor do their results extend smoothly across taxa. Future studies should focus on species that are broad representatives of taxa, or play an especially important role in marine ecosystems. Similarly, within study species, experimenters should focus their efforts on traits that are more closely associated with fitness; while it is useful to demonstrate the impacts of climate change on certain traits, species survival depends on overall fitness, which consists of many interacting traits.

When examining multiple traits, another particular place to focus future efforts is in detecting evolutionary tradeoffs. Even if populations are able to adapt to future climate change, their adaptations often come at a cost to other fitness-related traits.

Thus, even if adaptation is possible, the tradeoffs incurred may preclude species survival. Finally, it is important to remember that evolutionary potential is only useful when found within populations of large enough size. Therefore, the most robust studies will need to include demographic information into survival projections for marine species.

Recent work in evolutionary potential has offered a glimmer of hope for marine organisms facing adverse environmental conditions in the near future. However, it is important to stress that this potential is not limitless, and should not deter from global efforts to reduce the effects of climate change in the future. Still, research in this field will provide useful information for projections under different future climate scenarios, and thus better inform management of marine resources.

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