REVIEW AND SYNTHESIS

Predicting evolutionary responses to climate change in the sea

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Abstract

An increasing number of short-term experimental studies show significant effects of projected ocean warming and ocean acidification on the performance on marine organisms. Yet, it remains unclear if we can reliably predict the impact of climate change on marine populations and ecosystems, because we lack sufficient understanding of the capacity for marine organisms to adapt to rapid climate change. In this review, we emphasise why an evolutionary perspective is crucial to understanding climate change impacts in the sea and examine the approaches that may be useful for addressing this challenge. We first consider what the geological record and present-day analogues of future climate conditions can tell us about the potential for adaptation to climate change. We also examine evidence that phenotypic plasticity may assist marine species to persist in a rapidly changing climate. We then outline the various experimental approaches that can be used to estimate evolutionary potential, focusing on molecular tools, quantitative genetics, and experimental evolution, and we describe the benefits of combining different approaches to gain a deeper understanding of evolutionary potential. Our goal is to provide a platform for future research addressing the evolutionary potential for marine organisms to cope with climate change.

INTRODUCTION

Global warming and ocean acidification are fundamentally altering the environmental conditions and biogeochemical processes of marine ecosystems. From near obscurity less than a decade ago, when relatively few examples were known (Richardson & Poloczanska 2008), the biological impacts of warmer oceans and ocean acidification (here collectively called climate change for simplicity) are now known to be large and pervasive (Harley et al. 2006; Hoegh-Guldberg & Bruno 2010; Doney et al. 2012). Strategies for documenting, understanding and attributing these impacts have varied from experimental, to modelling, to characterising long-term patterns of change. Experimental studies have provided crucial insight into the response of various attributes of marine species to higher temperatures (Portner & Farrell 2008) and ocean acidification (Kroeker et al. 2013), but there is considerable scope for improvement in the design of these studies (Russell et al. 2012; Wernberg et al. 2012; Tatters et al. 2013). Modelling of both the rate and magnitude of physical changes, and the associated biological responses, has revealed a dynamic natural experiment in the sea with expected changes as dramatic or more so than those on land (Burrows et al. 2011; Sunday et al. 2012). Studies have also used ecological and physical data collected over decades or longer to explore the long-term effects of variations in ocean temperature and chemistry on the population ecology and community structure of marine ecosystems (Hawkins et al. 2008; Simpson et al. 2011). Shifts in species ranges and changes to phenology, abundance, life-history traits and physiological performance have all been identified and attributed to climate change (Doney et al. 2012; Poloczanska et al. 2013). These varied approaches have provided crucial insight into how organisms might respond to ongoing and future climate change, but fundamental knowledge gaps remain (Kelly & Hofmann 2013).

A major goal of climate change research is to determine whether individual populations and communities will persist and be maintained at levels that are similar to, or different from, today. To meet this goal, models of population persistence and community dynamics must be parameterised with data on the performance of species and their ecological interactions under future conditions. Intense effort by physiologists and ecologists has rapidly generated a rich database of estimates of performance under a range of future conditions, permitting the development of data-driven models that were impossible just a few years ago (e.g. Ling et al. 2009; Cheung et al. 2011). Nevertheless, most projections of species persistence in marine habitats preclude the role of evolution and the scope for organisms to adapt to climate change. Ecological projections are an essential first step, but projections that exclude evolutionary

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considerations are likely to misestimate the impact of climate change (Pandolfi *et al.* 2011). While studies estimating evolutionary responses to climate change in marine systems are still relatively scarce, experimental approaches are increasingly being applied to understand adaptation to climate change in terrestrial ecosystems (Bradshaw & Holzapfel 2006; Hendry *et al.* 2011; Hoffmann & Sgro 2011; Shaw & Etterson 2012). Furthermore, there have been important theoretical advances in understanding the roles of phenotypic plasticity and genetic evolution in species persistence in the face of climate change (e.g. Lande 2009; Chevin *et al.* 2010; Bonduriansky *et al.* 2012). As such, marine biologists have much ground to make up in providing estimates of the impacts of climate change that include evolutionary processes.

We suspect several reasons for this lag in studying evolutionary responses to climate change in marine systems; relative to terrestrial biology: (1) marine biology has a weak tradition of predicting micro-evolutionary change via traditional quantitative genetics techniques (compare the number of marine versus terrestrial examples in classic quantitative genetics texts such as Lynch & Walsh 1998), (2) there are relatively fewer marine model species for evolutionary research and (3) many marine organisms are less amenable to multigenerational studies of experimental evolution. Here, our goals are to emphasise why an evolutionary perspective is crucial to our understanding of the impacts of climate change in marine systems and to provide an overview of the types of approaches that may be particularly useful for estimating the evolutionary potential to cope with climate change in the sea.

The importance of an evolutionary perspective

Without an evolutionary perspective, it is difficult to predict the trajectory of biological responses to environmental change over time. Massive losses of biodiversity and ecosystem collapse are forecasted (e.g. Veron 2008; Frieler *et al.* 2013) and climate change has contributed to extinction in the geological past (Kiessling & Simpson 2011). While there is legitimate concern that the rate of environmental change exceeds the capacity for many species to adapt (Parmesan 2006), theoretical models show that even species with relatively long generation times might adapt to environmental change if their populations have sufficient standing genetic variation and the potential for a high intrinsic rate of growth (Chevin *et al.* 2010; Gienapp *et al.* 2013). There is also theoretical evidence that non-genetic mechanisms, such as heritable epigenetic changes, may enable populations to adapt faster than otherwise expected (Geoghegan & Spencer 2012; Klironomos *et al.* 2012). Therefore, a consideration of evolutionary potential is crucial in attempting to predict the future impacts of climate change for a range of organisms.

Numerous examples have shown that evolution can be remarkably rapid, even for species that live for many years (Hendry *et al.* 2011; Sanford & Kelly 2011; Shaw & Etterson 2012). Therefore, it is no longer tenable to argue *a priori* that evolution only occurs over timescales that are dramatically different to the present pace of environmental change. Furthermore, phenotypic plasticity is increasingly being found to contribute strongly to persistence in the face of climate change (Charmantier *et al.* 2008; Anderson *et al.* 2012; Barrett & Hendry 2012). Importantly, phenotypic plasticity may help buffer populations against the immediate impacts of changed environmental conditions and provide time for genetic adaptation to catch up (Chevin *et al.* 2010). We suggest that both phenotypic plasticity and genetic adaptation will play key roles in modifying the impacts of climate change on marine organisms, that they could interact in important ways, and that both must be estimated.

One of the usual ways of estimating the impacts of climate change on marine populations is analogous to an acute ecotoxicological approach: individuals are sampled from the field, exposed to some predicted future change in temperature, acidity or both, and then tested for the exposure's impact on some metric of performance, such as survival, growth or behaviour (Byrne 2011). While these studies have been crucial for identifying the potential short-term impacts of climate change and the life-history stages that may be most vulnerable, they tell us less about the likely impacts of this change over multiple generations in the real world. For example, if 60% of individuals in an experiment perish after exposure to environmental conditions that are projected for 2100, does that mean the source population is likely to decline to the point of extinction? Perhaps, but an evolutionary biologist could take a more optimistic view: the surviving 40% of individuals suggests that the population may harbour sufficient variation to adapt to such conditions, leading fewer individuals in the next generation to suffer mortality under the same conditions. In this case, failing to consider evolution will lead to an overestimation of the impacts of climate change over multiple generations. On the other hand, ecological processes can magnify the effects of seemingly minor changes in fitness: the surviving 40% of individuals in the above experiment may persist in the laboratory, but their poorer condition might make them particularly susceptible to competition or predation in the wild. In this case, laboratory studies risk underestimating the impacts of climate change. How can we improve our predictive ability? Understanding the capacity for adaptation requires elucidating the sources of variation among individuals and populations to determine if they possess sufficient genetic variation upon which selection can act, and/or testing their capacity to generate new genetic variants. However, even this approach may prove misleading if demographic parameters are not considered. Populations may adapt to climate change, but too slowly to avoid extinction if they decline to critically small sizes in the meantime (Bell 2013). Ultimately, predicting the persistence of populations and species in a rapidly changing climate will require coupling estimates of evolutionary potential to demographic processes (Hoffmann & Sgro 2011; Gonzalez *et al.* 2013).

In this review, we first consider what the geological record and present-day analogues of future climate change can tell us about the potential for adaptation to climate change in the sea. Next, we examine the experimental evidence that phenotypic plasticity may assist marine species to persist in a rapidly changing climate. We then outline various approaches that can be used to estimate evolutionary potential, focusing on molecular tools, quantitative genetic designs, experimental evolution and artificial selection. We discuss the strengths and limitations of each, plus the benefits of combining them to gain a deeper understanding of evolutionary processes. We consider the role that models of evolutionary rescue, which explicitly combine both ecological (demographic) and evolutionary processes, may play in predicting the consequences of climate change for marine biodiversity. Finally, we make some preliminary observations about key issues facing managers seeking to maintain evolutionary potential within marine ecosystems.

THE GEOLOGICAL RECORD AND PRESENT-DAY ANALOGUE ENVIRONMENTS

Is there evidence of persistence in the face of the stressors associated with climate change? Here, we consider two sources of evidence: the fossil record (that can provide a survey of those species that did or did not adapt to a changing environment) and present-day environments that mimic expected future conditions (that can suggest which species may be capable of adapting or acclimating to changing conditions).

The geological record

The fossil record has long held pride-of-place among biologists interested in the evolutionary history of life. Much of that history is characterised by evolutionary response to dramatic changes in climate and many other environmental changes (Culver & Rawson 2000). Recent focus on the effects of climate change on extant ecosystems, and the recognition that short-term experiments may not extrapolate into longer term climatic adaptation, have re-invigorated the study of climate change in Earth's history, including organismal response to catastrophic changes in ocean temperature and acidity (Pandolfi *et al.* 2011). For example, both Knoll *et al.* (2007) and Kiessling & Simpson (2011) found non-random extinctions among calcified organisms responding to dramatic changes in climate over the geological record – while calcified animals were more vulnerable overall, those with more buffered skeletal mineralogy were more resistant to environmental events that involved increased pCO_2 than those with less buffered skeletons. Conversely, Hannisdal *et al.* (2012) found that coccolithophores were larger, more heavily calcified and more common and widely distributed in the pre-34 Ma greenhouse world, and declined along with pCO_2 during the Oligocene (34–23 Ma). More recently, Kiessling *et al.* (2012) found equatorial reductions in coral biodiversity associated with increased sea surface temperatures during the last interglacial, 125 ka. These results demonstrate that palaeontological studies can offer valuable insights into the responses of different groups of marine organisms to major climatic changes.

However, the fossil record has its limitations. Data from the fossil record are generally limited in temporal resolution, with the pace of both evolution and climate change often being faster than the pace at which fossils are incorporated into the record. Consequently, inferring causal interactions between evolution and climatic changes can be elusive due to this mismatch of time scales. Moreover, the relatively small proportion of organisms that do fossilise means that response to climate change can be studied only from a biased subset of marine organisms. Limitations to the taxonomic resolution of some fossil organisms may also make it difficult to distinguish evolution of morphological adaptations from species succession within communities (e.g. Hannisdal *et al.* 2012). Preservation is also usually limited to morphological components, so changes in physiology can only be inferred. As a result, many important evolutionary responses to climate change (e.g. changes in physiology and phenology) may go undocumented. Nevertheless, elucidation of the detailed response of individual clades during highly constrained climate events has the potential to provide important insights into the tempo and mode of evolutionary response to climate change when conducted at the appropriate temporal scales.

Present-day analogue environments

Another way to investigate potential evolutionary responses to climate change is to take advantage of geographical regions (e.g. thermal hotspots) or local environmental anomalies (e.g. CO_2 seeps) that already experience temperature or acidity levels that tend to mimic the predicted future conditions for the ocean. By studying the communities that live there, it might be possible to make some predictions about which species or groups of organisms are likely to be successful and which will not (Fabricius *et al.* 2011). Certainly, there are numerous examples of local adaptation (Marshall *et al.* 2010; Sanford & Kelly 2011), and the performance of species in extreme environments can illustrate the scope for adaption in different groups. For example, some corals survive and grow in the Persian Gulf, where water temperatures already exceed the upper range of climate change predictions for most other locations (Coles & Riegl 2013). Comparing the performance of organisms along geographical clines, such as latitudinal temperature gradients, may also provide good evidence of the capacity for acclimation and adaptation to altered environmental conditions (Somero 2005; Sanford & Kelly 2011).

While these approaches can be informative, they also have their limitations, and they are not necessarily a clear guide to biological responses to future change. It is possible that the rate of evolution in the studied populations may have been very different from that required to keep pace with contemporary climate change. Furthermore, these locations may experience other environmental anomalies that confound attempts to use them as reference sites. For example, in addition to very high summer temperatures, Persian Gulf populations also experience very low winter temperatures; therefore, marine populations may be adapted to a highly variable thermal environment rather than a warmer environment *per se*. Similarly, geographical locations that are naturally acidified due to upwelling of CO_2 rich water might be representative of future ocean chemistry (Manzello 2010), but they are also rich in nutrients that can facilitate calcification at low aragonite saturation (Holcomb *et al.* 2010). Consequently, they might not be ideal analogues of future ocean conditions at other locations.

Localised anomalies (e.g. CO_2 seeps) may be better analogues of future conditions if they do not suffer from additional confounding variables as discussed above, and the biological communities in these areas are a mixture of species that appear to be doing well and others that are negatively affected (Hall-Spencer *et al.* 2008; Fabricius *et al.* 2011). Unfortunately, these studies have their own limitations due to their small spatial extent. The area comprised in these localised anomalies is far smaller than the average dispersal distance for most marine organisms. Consequently, populations living at these sites could be composed of individuals that are recruited from nearby populations that have been selected to live under present-day conditions. Populations currently living under the modified conditions are unlikely to mimic fully the response of future ecosystems for two reasons. First, they may be maintained by an external source of recruits, making extinction less likely. Alternatively, they are likely to be swamped by individuals that are not adapted to the modified conditions, and will experience significant migration load, hampering their ability to evolve.

Despite these limitations, the fossil record and studies of present-day environmental analogues provide circumstantial evidence for the *potential* for marine organisms to cope with rapid climate change

and stressful conditions. Some species appear to be successful in adapting to rapid change, while others do not. However, in order to gain a probabilistic prediction of evolutionary trajectories under climate change, direct tests are required. In the following sections, we suggest a number of useful approaches.

PHENOTYPIC PLASTICITY

Phenotypic plasticity has been identified as a crucial phenomenon that may allow organisms to persist in the face of environmental change and give populations the time to adapt to climate change (Chevin et al. 2010). For long-lived species, phenotypic plasticity is expected to be especially important, but it is likely to be an important component of adaptive responses for most species. Accordingly, a growing body of work has addressed the capacity of marine organisms to adjust their behaviour, physiology, or morphology in response to changed environmental conditions (Schulte et al. 2011). Thermal plasticity is commonly observed in temperate marine species (Somero 2005), which tend to experience a greater range of seasonal temperatures than tropical or polar species, and thus may be expected to have evolved the capacity to deal with such changes (Stillman 2003). Similarly, intertidal species are adapted to a highly variable environment and exhibit considerable thermal plasticity (Somero 2005). The same physiological or behavioural changes that enable organisms to cope with short-term natural environmental fluctuations can also be useful in coping with longer term climatic changes (Stillman 2003; Somero 2010).

Although plasticity is often expressed over days to weeks, in some instances it may require extended exposure to changed environmental conditions. For example, the cold water coral Lophelia pertusa exhibited a 26–29% reduction in calcification during a 1-week exposure to acidified seawater, but was able to maintain calcification during 6 month incubations in conditions that would normally be expected to cause dissolution (Form & Riebesell 2012). Similarly, Dupont et al. (2013) found that fecundity of female sea urchins declined dramatically after 4 months exposure to acidified seawater, but returned to control levels after 16 months. These studies demonstrate the need for more long-term experiments in marine climate change research. Many experiments on the effects of global warming and ocean acidification are conducted for just a few days or weeks, which may be inadequate to capture the within-generation capacity for organisms to adjust to environmental change and could lead to erroneous conclusions about long-term impacts.

Phenotypic plasticity can also involve permanent responses to the environment that are established during ontogeny. In this case, plasticity is only expressed if the organism experiences the environmental stimulus during early life. Developmental plasticity is widespread among animals (West-Eberhard 2003), and is especially important to climate change research, because individuals in the future will experience changed climate conditions throughout life. Although the critical role of temperature in developmental processes of marine organisms is well known (O'Connor et al. 2007), few studies have considered this in the context of acclimation to climate change. In one of the few studies conducted to date, Donelson et al. (2011) found that fish reared from early life at 3 °C above average summer temperatures exhibited a smaller increase in metabolic rate at the higher temperature compared with fish that were first reared at control temperatures and then swapped to the warmer temperature later in life. Similar critical effects of developmental temperature on ther-

mal acclimation abilities in adults have been demonstrated in freshwater fishes (Scott & Johnston 2012). Given the widespread occurrence of developmental plasticity in behavioural and life-history traits of some marine species (Warner 1997), we predict that this will be an important mechanism by which many marine species cope with future changes in temperature and other environmental conditions.

Plasticity not only depends on the conditions an organism experiences with its own lifetime, but can also depend on the conditions experienced by previous generations (Burgess & Marshall 2011). There is increasing evidence that the environmental conditions experienced by parents has a significant effect on the performance of the offspring, through the transmission of nutritional, somatic, cytoplasmic or epigenetic material between generations (Bondurianski & Day 2009; Marshall & Morgan 2011; Klironomos et al. 2012). Although parents stressed by extreme environmental conditions may produce inferior offspring, there is emerging evidence that transgenerational effects can also have positive effects on the performance of offspring that experience the same conditions as their parents (Salinas & Munch 2012), and that these effects can extend to predicted future climate conditions (Burgess & Marshall 2011; Donelson et al. 2012; Miller et al. 2012). For example, juvenile damselfish were able to compensate completely for the negative effects of elevated water temperature on metabolic rate and aerobic scope when their parents were also reared at elevated temperatures (Donelson et al. 2012; Fig. 1). Similarly, negative effects of ocean acidification on growth, development and survival of larval Sydney rock oysters were reduced when they were spawned from adults exposed to high CO_2 (Parker et al. 2012). These new studies demonstrate the critical importance of including the potential for transgenerational plasticity in experimental assessments of climate change impacts, especially studies on early life-history stages.

Many experimental studies focus on early life-history stages because they tend to be most sensitive to environmental change (Byrne 2011). However, these life-history stages are also the most likely to benefit from transgenerational plasticity. Consequently, the conclusions drawn about the sensitivity of early life-history stages to climate change can critically depend on whether parents have experienced the same conditions. Although cross-generational experiments with marine species have traditionally been considered challenging, spawning and rearing conditions have now been established for many marine taxa. This opens the way to include transgenerational effects into marine climate change studies (see Bonduriansky et al. 2012 for discussion on experimental design). In some instances, it is possible that transgenerational plasticity will only be fully expressed if the parental population has also had the opportunity for developmental acclimation (Donelson et al. 2012). In this case it may take at least two full generations to express all the plasticity available in response to changed environmental conditions. Such studies are laborious, but necessary if we are truly to understand the scope for phenotypic plasticity to assist organisms to cope with a changing climate over coming decades.

MEASURING EVOLUTIONARY POTENTIAL

A trait's evolutionary potential depends on how much it varies genetically. For traits determined by one or few genes, genetic variation can be measured in terms of the allelic variants uncovered by molecular markers (Rockman 2012). For traits determined by multi-
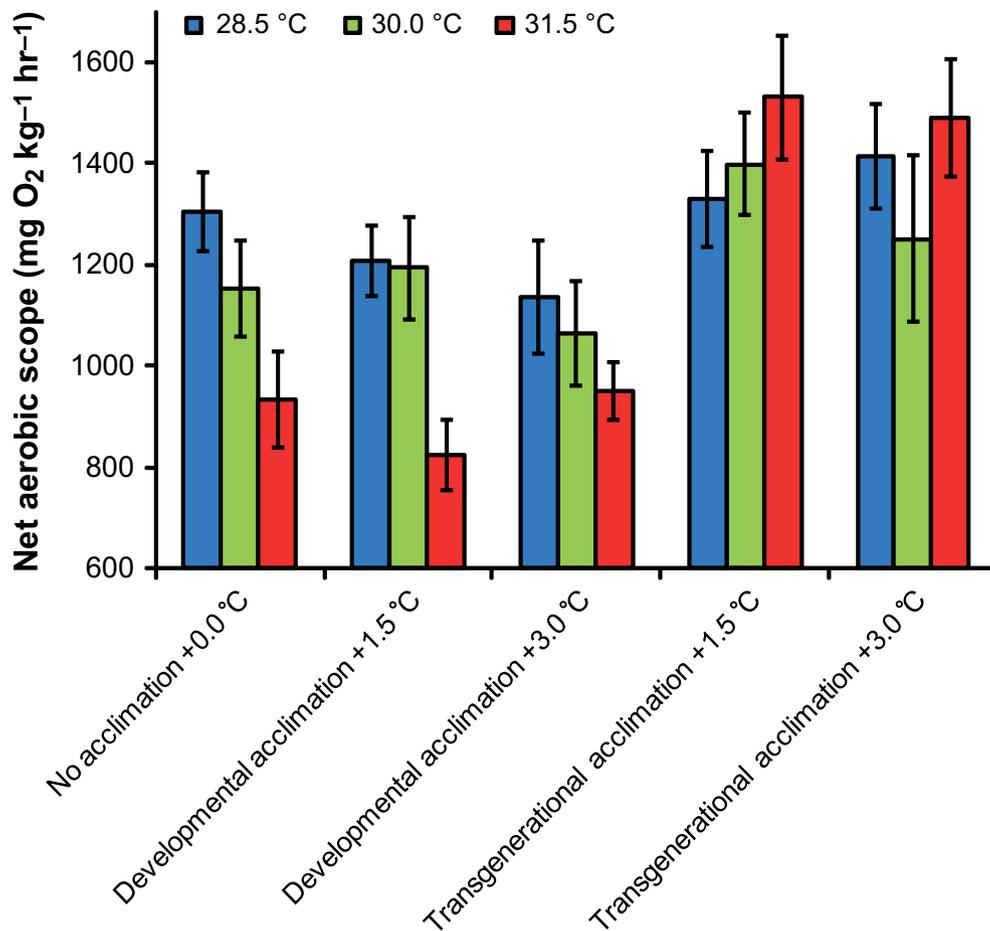
Figure 1 The effect of predicted global warming on the aerobic scope (the difference between resting and maximum rate of oxygen consumption) of the coral reef fish *Acanthochromis polyacanthus* is dependent on the thermal environment experienced during early development and also by the parents. Aerobic scope declines sharply in juveniles reared under current day conditions and then exposed to temperatures 1.5 °C and 3.0 °C above the summer average (no acclimation group). When juveniles are reared at elevated temperatures from hatching, there is no significant improvement in aerobic scope (developmental acclimation groups). However, aerobic scope is fully restored in juveniles from parents that were also reared at 1.5 °C and 3.0 °C above the summer average (transgenerational acclimation groups). This illustrates that it may take two generations for the full extent of thermal plasticity in aerobic scope to be expressed. From Donelson *et al.* 2012.

ple genes (so-called polygenic or quantitative traits), genetic variance is often measured as heritability (the fraction of total phenotypic variation that is due to genetic causes). For quantitative traits, evolutionary potential is also measured as the expected response to selection across generations (Lynch & Walsh 1998), which predicts not only whether they can evolve, but also evolve adaptively under a known selection regime.

Of the many approaches to measuring evolutionary potential, all have strengths and limitations (Table 1). Some (e.g. experimental evolution) are increasingly being used to predict how marine populations may respond to the novel conditions and selection pressures arising from climate change, while others (quantitative genetics) remain less utilised. We therefore provide an overview of the main categories (molecular approaches, quantitative genetic approaches, experimental evolution and artificial selection), illustrated with relevant examples from the marine literature, in the hope of encouraging more researchers to consider using them. We deal with these categories separately, but end the section by outlining how the greatest inferential power lies in combining approaches from each.

The framework in which we present these approaches is adopted from Phillips (2005), whereby phenomenological, quantitative genetic approaches are viewed as 'top down' and mechanistic, molecular approaches are viewed as 'bottom up'. Under this view, quantitative genetics provides the most direct way of estimating heritable variation in the polygenic traits likely to be most relevant to adaptive evolution, but provides the least precision or information about the underlying genetic mechanisms (Fig. 2). On the other hand, molecular approaches can provide precise estimates of molecular variation in certain traits of interest and their mechanistic basis, but may not directly estimate the heritability of polygenic traits (Fig. 2).

Molecular approaches

The revolution in molecular biology provides some truly remarkable tools for examining the underlying genetic changes in populations and individuals experiencing different environmental conditions and holds great promise for estimating evolutionary potential (Edwards 2013). These tools are increasingly being folded into studies of marine climate change. Molecular tools can document molecular changes within lineages, identify gene activation under different conditions, and determine molecular pathways underlying the

Table 1 The various approaches to measuring evolutionary potential, with strengths, limitations, relevant organisms and some examples from the marine literature

Approach	Strengths	Limitations	Relevant organisms	Examples
Molecular/ genomics	Can survey populations for molecular variation (i.e. among individual alleles) Can give insight into mechanisms of gene expression Can be applied to natural populations	Genotype–phenotype map often poorly resolved: difficult to link allelic variation to heritable phenotypic variation in quantitative traits that are likely to be most relevant in adaptive evolution May not predict evolutionary potential unless applied to individuals of known pedigree (in which case, some of the limitations of quantitative genetic approaches also apply)	All organisms, especially large, long lived or rare species that are not amendable to laboratory breeding experiments or experimental evolution	Barshis *et al.* 2013; Pespeni *et al.* 2013;
Quantitative genetics	Can survey populations for phenotypic variation (and partition it into heritable and non-heritable components) in quantitative traits that are likely to be most relevant in adaptive evolution Can predict evolutionary potential based on a single generation Can be applied to natural populations once individuals of known pedigree are obtained through an appropriate breeding design	Genotype–phenotype map often poorly resolved: difficult to link heritable phenotypic variation to underlying allelic variation or mechanisms of gene expression Use in multigenerational forecasts assumes constant selection and constant genetic variance, which may not hold for natural populations Breeding designs may be challenging to implement, and impractical for some life-histories (e.g. brooders or long-lived species) Heritable components of variation include both beneficial and deleterious allelic effects, and may be biased by non-genetic effects that are beyond experimental control Large sample sizes needed at the sire or family level for adequate inferential power	Best suited to broadcast spawners with no parental care that can be reared in captivity (e.g. many echinoderms, molluscs, crustaceans and fish) Fragmentation studies suited to clonal species (e.g. corals, ascidians, bryozoans, sponges)	Kelly *et al.* 2013; Foo *et al.* 2012; Sunday *et al.* 2011; Pistevos *et al.* 2011;
Experimental evolution and artificial selection	Can track or test hypotheses about realised (instead of potential) evolutionary processes, based on multiple generations	The time required to follow multiple generations may be prohibitive May rarely be feasible to apply to natural populations Not practical for large, long-lived organisms	Best suited to organisms with small size, short generations, limited dispersal and amenable to laboratory culture (e.g. many phytoplankton and some zooplankton)	Kelly *et al.* 2012; Lohbeck *et al.* 2013; Jin *et al.* 2013;
Combined approaches	The best of all worlds: can link pattern and process in predicting evolutionary potential or explaining realised evolutionary change	The worst of all worlds: costs (time, effort and money) may limit sample size, to the point of risking inferential power	Combinations from above	Runcie *et al.* 2012

expression of different traits. For example, Pespeni *et al.* (2013) found that larval morphology and development in the purple sea urchin showed little response to elevated CO_2, but detected signatures of genetic change across hundreds of loci. Such shifts in the frequency distribution of the transcriptome reveal the potential for populations to adapt to climate change, even when they show few outward signs of responding to such change. In a population genomic study, Barshis *et al.* (2013) found differences in genome expression between corals that were sensitive or resilient to thermal stress. Conspecifics of both types up-regulated the expression of various thermal-response genes, but thermally resilient corals did so more strongly than thermally sensitive corals, suggesting the presence of genetic variation for thermal tolerance within the population. Studies such as these demonstrate the potential for genomic tools to detect genetic variation that may potentially fuel adaptive responses to climate change, and identify the likely cellular mechanisms involved (Table 1).

Genomic tools are constantly decreasing in cost and gaining in accessibility for non-model organisms. Furthermore, such tools free researchers from a number of major constraints that traditional approaches suffer. For species in which controlled breeding is impossible (e.g. most large or long-lived marine organisms), molecular approaches may be the only practical way of estimating whether genetic variation in a trait of interest exists (Edwards 2013). Similarly, population genomics offers a useful way of identifying signatures of genetic evolution and local adaptation to environmental change in organisms for which traditional approaches for testing local adaptation (e.g. transplants; Howells *et al.* 2013) are impractical. In addition to such immediate benefits of molecular approaches, there are broader benefits to this growing research effort. As work on the molecular basis of adaptive responses to climate change accumulates, we may become more able to identify common genetic and physiological mechanisms underlying such responses and extrapolate them to other species that have not been studied directly.
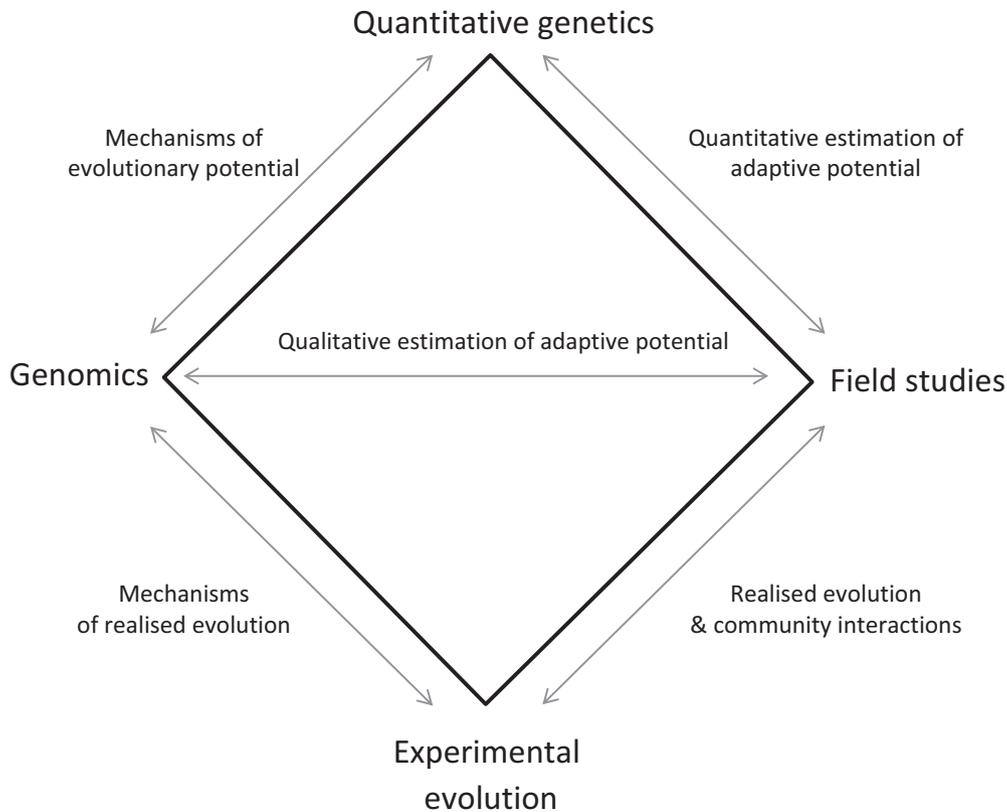
Figure 2 Schematic of the different approaches for understanding the potential role of evolution in determining the impacts of climate change in marine systems. Each approach is best suited to answering a specific question about the adaptive potential of marine population, but in isolation yields incomplete understanding. Combined approaches will generate the greatest insight into the potential for adaptation to climate change, and the mechanisms involved, but combining all approaches is logistically impossible for almost any system.

Molecular approaches do, however, have notable limitations: most importantly, they may not provide estimates of the heritable variation in polygenic trait/s that will likely be of most interest in predicting adaptive responses to climate change (but see Edwards 2013). As such, molecular approaches may preclude the direct integration of the data they generate with predictive models of evolutionary change and evolutionary rescue. There have been previous assessments of the efficacy of molecular approaches for predicting evolutionary change that we will not repeat here (e.g. Hendry *et al.* 2011; Travisano & Shaw 2013), but these approaches nonetheless represent an important pathway for examining the evolutionary potential of marine organisms, particularly when combined with experimental approaches (see below), or when other approaches are impractical.

Quantitative genetics

The field of quantitative genetics deals with the selection, inheritance and evolution of quantitative traits, which are the vast majority of those relating to whole-organism phenotypes. They include morphological, physiological and behavioural traits, which in turn determine life-history traits such as survival and reproduction, and the ultimate trait of individual fitness (Lynch & Walsh 1998; Conner & Hartl 2004). Typically, quantitative genetic approaches aim to predict phenotypic evolution across single generations using specific

breeding designs or pedigrees to partition a trait's total phenotypic variation into its causal components (e.g. additive genetic effects, maternal effects). For a comprehensive treatment of this topic, we recommend Lynch & Walsh (1998). However, for the purposes of this review we focus on quantitative genetic designs that are particularly well suited to marine life-histories and the study of stressors associated with climate change.

Diallel breeding designs involve cross-breeding a number of males and females, such that every male is mated with every female (Fig. 3). Under such a design, phenotypic variation among offspring is partitioned into variation due to fathers ('sires' in the quantitative genetics literature), variation due to mothers ('dams'), variation due to the interaction between maternal and paternal inheritance, and non-genetic environmental variation. Because sires are assumed to contribute little more than genes to their offspring (an increasingly problematic assumption; see below), the sire component of variation in any offspring trait is viewed as additive genetic variation in that trait. Diallel designs have been used in a range of systems to great effect, but their use is particularly suited to the study of marine organisms, because many are broadcast spawners that shed both eggs and sperm externally. This is ideal for diallel breeding designs because ejaculates of sperm and clutches of eggs can be repeatedly subdivided and crossed together such that the sperm of each male can be crossed with the eggs of many different females at the same time (and vice versa for females). A modified version of this
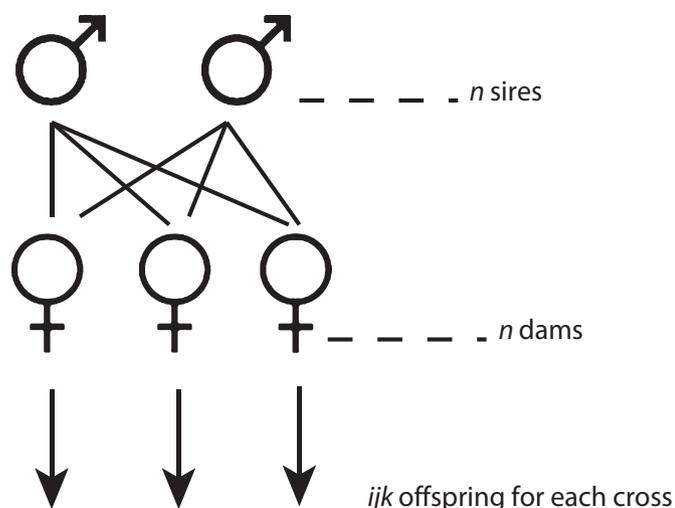
Figure 3 Illustration of a diallel cross, where *n* males are each crossed with *n* females and the trait of interest is measured in replicate offspring. Phenotypic variation of the offspring is then partitioned into variation due to fathers (sires), variation due to mothers (dams), variation due to the interaction between maternal and paternal inheritance, and non-genetic environmental variation. The variation in offspring associated with fathers is considered the heritable genetic component of that trait.

approach (the North Carolina II) has been used to great effect to estimate genetic variation in marine invertebrates (e.g. Galletly *et al.* 2007), and fishes more generally (Johnson *et al.* 2010), while new studies are beginning to use this approach in relation to climate change specifically (Sunday *et al.* 2011; Foo *et al.* 2012; Kelly *et al.* 2013). For example, Kelly *et al.* (2013) used a dialell design to estimate the heritability of larval size under different future low-pH conditions. They found significant additive genetic variation in this important trait and were able to integrate this estimate into a simple model of evolutionary change. Importantly, they found that integrating this estimate of heritability into their model changed projections of future population growth rates by up to 50%.

An alternative to diallel breeding designs takes advantage of the clonal life-history of many marine organisms. Clonal taxa (e.g. seaweeds and colonial invertebrates, including corals, ascidians, bryozoans and sponges) dominate many marine habitats and have the unifying feature of modularity, which often allows genetic individuals to be replicated by fragmentation (Monro & Poore 2005). Fragmentation offers a simple way to estimate a trait's heritability in the broad-sense (including additive and non-additive genetic effects) by partitioning its total phenotypic variation into within- and among-genotype components (Lynch & Walsh 1998). The main limitation of the approach is that the latter component may be biased by non-genetic effects (e.g. common environmental effects) that are challenging to account for experimentally (but see Lynch & Walsh 1998: pp. 592–5). The main advantage is its simplicity and tractability to field studies, or studies involving long-lived species that are unsuited to breeding designs. While the use of fragmentation designs in marine systems is generally rare, Pistevos *et al.* (2011) used such a design to estimate the broad-sense heritability of several life-history traits in the bryozoan, *Celleporella hyalina*, under predicted changes in temperature and CO_2. They found that different clonal lines had very different responses to such changes, indicating that this species has some potential to

adapt to climate change. In another fragmentation study on *Acropora* corals and their algal symbionts, Császár *et al.* (2010) detected high broad-sense heritabilities for thermal tolerance traits in the symbionts, but much lower heritabilities for analogous traits in the host corals, indicating a potential mismatch in adaptive potential within the coral holobiont.

Traditional quantitative genetic approaches are not without serious limitations (Table 1). First, they require that species can be bred under controlled conditions to establish a pedigree, or that they can be fragmented. For many species, this requirement will be difficult to meet, limiting the scope to apply such approaches. Second, quantitative genetic approaches make assumptions about the ability to measure genetic variance. Diallel designs assume that all of the variance associated with sires is additive genetic variance – an assumption that is increasingly called into question by evidence of non-genetic (epigenetic) inheritance in many taxa (Bonduriansky & Day 2009). Similarly, fragmentation designs cannot distinguish between additive and non-additive genetic variance, and versions of these designs that fail to account for parental effects make the overestimation of genetic variation almost inevitable (Lynch & Walsh 1998). More pragmatically, quantitative genetic approaches may be limited by their costliness, given they are highly labour-intensive. Designs that include fewer than 20 sires or genotypes are unlikely to have sufficient power to detect genetic effects (Conner & Hartl 2004); consequently, thousands of individuals of known parentage may need to be tracked in appropriately replicated designs. Such designs may well be beyond some research programmes and budgets. A broader limitation of quantitative genetic approaches is their inherently phenomenological nature. This is because the complex genetic basis and environment-dependent expression of most quantitative traits makes it often impossible to map phenotypic variation to the underlying genotypes of individuals (Rockman 2012). Consequently, such approaches provide little information about precise modes of gene action, limiting their ability to yield broader insights into how genetic adaptation is likely to proceed. Finally, unless all of the traits that covary genetically with each other and fitness are measured, quantitative genetic experiments are likely to overestimate the evolutionary potential of a population. Solutions to this 'missing trait' problem require estimating total fitness, which is notoriously difficult (Lynch & Walsh 1998; Conner & Hartl 2004). Despite these potential limitations, quantitative genetics is still the most direct way to estimate heritable variation in traits that are relevant to climate change adaptation, can be done within a single generation, and provide information on genetic variation that can readily be used in models of population trajectories through time (see below).

Experimental evolution and artificial selection

Thus far, we have discussed single-generation approaches to measuring evolutionary potential. While such approaches offer more insight into the likelihood of marine populations adapting to climate change than ecological or physiological studies that ignore this potential, the implausibility of measuring all traits that will be relevant to adaptation makes such approaches unlikely to predict this process perfectly. An alternative approach is to subject laboratory populations to the conditions associated with climate change for multiple generations and compare the response of these populations to that of control populations. These approaches make no assump-

tions about the mode of inheritance and integrate the role of phenotypic plasticity in determining the magnitude of evolutionary change. The approach is especially well suited to organisms with rapid generation times (Collins & Bell 2004; Reusch & Boyd 2013). Experimental evolution has been used with considerable success in evolutionary biology, with many studies identifying a remarkable capacity to evolve in response to environmental stressors including warmer temperatures and pH change (Futuyma & Bennett 2009). Those studies that have conducted experimental evolution in marine systems have shown that some organisms have considerable capacity to evolve in response to climate change (Lohbeck *et al.* 2012; Jin *et al.* 2013), but that this capacity is not unlimited (Lohbeck *et al.* 2013), and studies of microalgae show that evolutionary changes are not always adaptive (Collins & Bell 2004). Experimental evolution experiments may be founded with a single genotype (clone), which is useful for testing the rate of adaptation by genetic mutation, or with multiple genotypes, which takes into account selection on existing genetic variation. As expected, evolution in such experiments proceeds faster when they include selection on existing genetic variation (Lohbeck *et al.* 2012). Those wishing to predict the potential for adaptation to climate change should take care to replicate at the scale of selection lines (the true unit of replication in such studies), and should found their selection lines with as many individuals as practical, within the limits of the experimental design, so as to capture as much initial standing genetic variance as possible in experimental populations.

A subtle but important variation on experimental evolution is to conduct artificial selection. While in experimental evolution studies, researchers usually manipulate the environmental conditions that select the individuals to contribute to the next generation, artificial selection involves the researcher actively choosing these individuals based on their specific phenotype (see Fry 2003 for a full delineation of the benefits and costs of each approach). Artificial selection experiments are valuable for understanding evolutionary responses to climate change (Reusch & Boyd 2013) and, in particular, will identify correlated responses to selection that may not have been anticipated. Artificial selection has been highly successful in testing for evolutionary trade-offs, whereby adaptive improvement in one trait comes at the expense of performance of another trait (Fry 2003).

The growing list of studies that have used experimental evolution to study evolutionary responses to climate change in marine populations is providing evidence that some species can evolve rapidly to cope (e.g. Lohbeck *et al.* 2012; Jin *et al.* 2013;), whereas others have more limited potential to adapt (Kelly *et al.* 2012). Experimental evolution and artificial selection are by far the most direct and powerful ways of estimating the evolutionary potential of a focal population. They also offer opportunities to test how adaptation could affect the outcome of ecological interactions between species (Tatters *et al.* 2013) and how ecological interactions between species affect evolutionary potential (Collins 2011). Nevertheless, there are obvious limitations to this approach (Table 1). First, a species must have a sufficiently short lifespan for evolutionary change to actually be studied within a reasonable timeframe. While this requirement will be met by many species, some of the most environmentally- and economically important species are too long-lived to be viable candidates. Second, experimental evolution approaches require that large populations be maintained in the laboratory since small populations will be too sensitive to the effects of genetic drift (Fry 2003;

Reusch & Boyd 2013). Consequently, only very small organisms are amenable to this approach. Even then, it may be possible to capture only a small proportion of the genetic variation present in natural populations in laboratory populations. Finally, like quantitative genetic approaches, experimental evolution may provide few insights into the mechanisms that underlie any observed evolutionary changes, again limiting the inferences that can be made for other species.

Combining different approaches – the best of all worlds

The approaches described above can be integrated with each other in ways that minimise their respective weaknesses. For example, combining molecular approaches with breeding designs places the molecular data into a heritability framework and provides more precise estimates of the mechanistic underpinnings of genetic variation in the traits of interest. Examples of such combined approaches are now emerging. In an elegant set of experiments, Runcie *et al.* (2012) combined a multi-environment breeding design with molecular analyses to estimate how temperature alters additive genetic variance in developmental gene expression of the purple sea urchin, *Strongylocentrotus purpuratus*. Interestingly, this study found strong genetic correlations in gene expression, but that downstream gene expression was largely buffered from changes in the expression of upstream regulator genes. Characterising variation in the molecular phenotype and the molecular signature of selection among different selection lines in experimental evolution studies would provide unprecedented insights into how organisms cope with climate change. We recognise that adding an additional layer to any one of these approaches exacerbates what is already a daunting and costly challenge. Nevertheless, a combined approach will yield insights that greatly outweigh the sum of their collective parts and our recommendation echoes similar calls in other fields to combine experimental and molecular approaches.

Can evolution rescue marine populations?

Recent theoretical and empirical work has shown that populations can evolve to cope with increasing stress over rapid time scales (~ 25 generations; Bell 2013). Termed 'evolutionary rescue', there is now an intense effort to parameterise models of population persistence with empirical estimates of population size and genetic variation (Gonzalez *et al.* 2013). The species for which evolutionary rescue models will be most appropriate are those with the greatest risk of extinction from climate change, including species with long generation times, small population sizes, ecological specialists and overexploited species (Dulvy *et al.* 2003). Species with very large populations and short generation times, such as most microorganisms, are generally at least risk of extinction, and thus may be less relevant to evolutionary rescue models. Preliminary attempts at modelling evolutionary rescue in marine populations has begun (Baskett *et al.* 2009; Sunday *et al.* 2011; Kelly *et al.* 2013), but we currently lack critical information about the genetic variation in responses to climate change. Specifically, Bell (2013) showed that estimates of genetic variation in response to a single stressor, or level of stress, are by themselves insufficient to accurately predict the potential for evolutionary rescue; rather, estimates of genetic correlations among levels or types of stress are necessary. For example, if there is a positive genetic correlation between perfor-

mance at low and high levels of stress associated with climate change, then models based on genetic variation in performance in high stress alone will dramatically *under*estimate the potential for evolutionary rescue (Fig. 4). Conversely, if there is a negative correlation between performance in the presence of one stress and another (e.g. performance in increased temperature and lower pH), then models based on genetic variation in one stress alone will dramatically *over*estimate the potential for evolutionary rescue (Fig. 4). Ultimately, for evolutionary rescue to occur there must be ample genetic variation in the dimension in which selection acts (Etterson & Shaw 2001). Accordingly, Baskett *et al.* (2009) incorporated a negative correlation between growth rate and tolerances to higher temperatures, though this trade-off was not based on formal estimates of additive genetic covariance between these two traits. While there are an increasing number of studies that estimate genetic variation in traits associated with coping with climate change, too few have quantified genetic correlations among important traits and we suggest this represents a crucial avenue of further research.

EVOLUTIONARY THINKING AND MARINE MANAGEMENT

The rate of environmental change will strongly affect the capacity of marine populations to persist for sufficiently long to adapt to climate change (Chevin & Lande 2010; Bell 2013). Thus, most importantly, taking global actions that slow the rate of climate change will diminish its impacts and maximise the potential for marine systems to adapt.

There are, however, some local actions that may increase the likelihood that marine systems can adapt to climate change. For example, larger populations are more likely to evolve and persist in the face of climate change for two reasons: first, because they have greater standing genetic variation (Frankham 1996), and second, because larger populations are less susceptible to drift that could prevent the spread of advantageous alleles through the population (Lynch 2010). Consequently, any management interventions that help maintain large populations will probably be beneficial in maintaining evolutionary potential. Fishing is one of the most obvious ways in which humans reduce marine population sizes. Fishing can also impose strong selection on marine populations (Conover & Munch 2002), which may reduce the capacity for adaptation to climate change if selection on traits from fishing is not in the same direction as selection for climate change (Fig. 4). Alternatively, climate change might accelerate evolution of populations in less desirable directions for fisheries (e.g. smaller body size, Cheung *et al.* 2013) if selection associated with climate change and fishing are positively correlated. Obviously, fishing is not the only anthropogenic factor that reduces population sizes: pollution and habitat destruction will also reduce the size of populations and, potentially, their capacity to evolve. Measures that limit the impact of these activities may carry the dual benefit of maintaining healthy populations in the current day and increasing the likelihood of maintaining viable populations in the future.

A major goal of management strategies is to conserve marine biodiversity. To determine the efficacy of these strategies into the future, it will be necessary to consider not only the ecological effects of climate change on populations but also to incorporate evolutionary potential and the demographic effects of selection into climate change assessments. Although not yet fully applied to marine populations, evolutionary rescue models have been used to
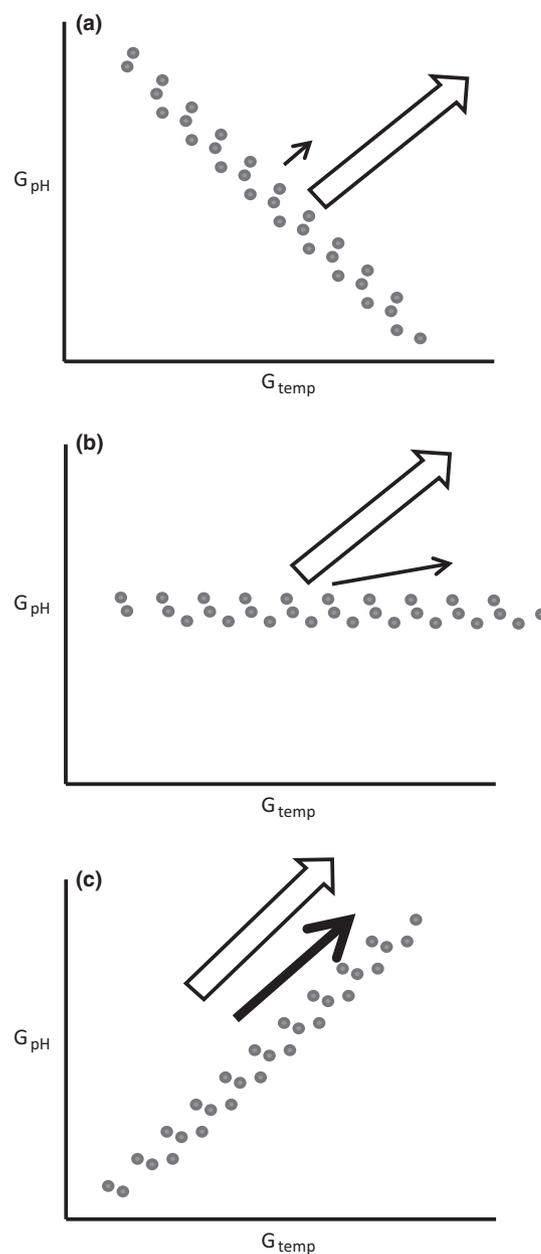

Figure 4 Genetic correlations can constrain responses to selection. This figure shows the additive genetic value (G) for traits associated with two environmental factors (temperature and pH) for a population (each dot represents an individual). The unfilled arrows show the direction and magnitude of selection acting on the mean of the population and the solid arrows show the direction and magnitude of the response to selection. In (a), there is little evolutionary response to selection because selection acts orthogonally to the direction of most of the genetic variation. In (b), the response to selection is biased towards the path of least genetic resistance because selection is not aligned with the direction of most genetic variation. In (c), there is unimpeded evolution because selection acts in the same direction as most of the genetic variation.

assess demographically sustainable rates of adaptation in plants (Kuparinen *et al.* 2010) and birds (Gienapp *et al.* 2013). Similar approaches may be especially useful in modelling the sustainability of fisheries under different climate change scenarios because the interacting effects of fishing mortality and evolutionary potential could be investigated in such models.

CONCLUSIONS

A major research effort over the past decade has demonstrated that many marine organisms living under current day conditions are sensitive to projected future environmental conditions. However, our ability to predict reliably the impacts of climate change on marine ecosystems is limited by an inadequate understanding of the potential of marine organisms to adapt to rapid climate change. We argue that a greater emphasis on testing the evolutionary potential of marine organisms is essential to understand the likely impacts of climate change on marine populations and to improve predictions about the effects of climate change on marine ecosystems more broadly.

Both phenotypic plasticity and genetic adaptation will be important in adaptive response to future climate change in the sea, and the potential for both must be estimated to understand evolutionary potential. Importantly, phenotypic plasticity may help populations persist in the short-term, which could buy time for genetic adaptation to progress in the longer term. Phenotypic plasticity is likely to be especially important for the persistence of species with relatively long generation times. Estimating the full potential for phenotypic plasticity in marine organisms will require multigenerational experiments that capture the potential for developmental and transgenerational plasticity. Long-term experiments are increasingly being used to test for plasticity within life-stages. However, future research needs also to consider the potential for environmental conditions experienced by previous generations, and during early development, to alter the response of individuals to environmental conditions predicted under climate change scenarios.

While the geological record and current-day analogues can provide tantalising glimpses into the effects of climate change over evolutionary time scales, we suggest that quantitative genetic approaches and experimental evolution hold the greatest prospects for predicting the capacity for genetic adaptation of most marine species over the timescales relevant to anthropogenic climate change. Diallel breeding designs and fragmentation studies are particularly well suited to estimating heritable phenotypic variation in many marine organisms and offer a powerful approach to explore the potential capacity for adaptation to keep pace with a rapidly changing environment. Experimental evolution studies are another powerful way to examine evolutionary responses to rapid climate change, and are particularly well suited to marine microorganisms. Modern molecular approaches are increasingly being used to establish if genetic variation to climate change exists within populations and identify the likely physiological pathways involved. Ultimately, the combination of several approaches (e.g. quantitative genetics and genomics, or experimental evolution and genomics) will provide the greatest inferential power by linking pattern and process in predicting evolutionary potential or explaining realised evolutionary change.

While we advocate an evolutionary perspective, it must be recognised that evolutionary potential is not a panacea for the widespread impacts of anthropogenic climate change. Increasing ocean temperatures and decreasing pH will have highly significant and widespread impacts on marine ecosystems over coming decades. Nevertheless, our ability to predict the extent of these impacts will be greatly improved by embracing an evolutionary perspective to the problem. An increased understanding of evolutionary processes will also assist in making decisions about the management of marine resources that offer the best opportunity for their sustainability into the future.

GLOSSARY

Evolution: Any genetic-based change in a population that is inherited from one generation to the next. It is said to be adaptive when driven by selection.

Genetic adaptation: The process by which a population evolves towards a phenotype that best suits the present environmental conditions.

Selection: The non-random differential survival or reproduction of individuals with different phenotypes.

Genetic variation: The presence in a population of more than one allele at a locus. Alleles are alternative forms of the same gene, while a locus is a specific site in the genome containing one or more genes.

Acclimation: The altering of physiological, behavioural, or morphological characteristics through phenotypic plasticity to better suit an environment.

Phenotypic plasticity: The capacity of individual genotypes to produce different phenotypes when exposed to different environmental conditions.

Developmental plasticity: Irreversible phenotypic plasticity resulting from environmental cues experienced during development.

Transgenerational plasticity: Phenotypic plasticity resulting from environmental cues experienced during the parental, or previous, generations. It can occur via epigenetic inheritance or through the transmission of nutrition, proteins, hormones or other bioactive materials from parents to their offspring.

Quantitative genetics: The study of the selection, inheritance and evolution of continuously varying traits that are determined by multiple genes.

Experimental evolution: The use of controlled experiments to study evolution. Populations are exposed to new environmental conditions for many generations to observe if they adapt genetically to those conditions.

Evolutionary rescue: The recovery of populations, through genetic adaptation, from demographic effects caused by environmental change that would otherwise cause extinction.

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