CHAPTER TWO

Acclimatization and Adaptive Capacity of Marine Species in a Changing Ocean

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Abstract

To persist in an ocean changing in temperature, pH and other stressors related to climate change, many marine species will likely need to acclimatize or adapt to avoid extinction. If marine populations possess adequate genetic variation in tolerance to

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climate change stressors, species might be able to adapt to environmental change. Marine climate change research is moving away from single life stage studies where individuals are directly placed into projected scenarios ('future shock' approach), to focus on the adaptive potential of populations in an ocean that will gradually change over coming decades. This review summarizes studies that consider the adaptive potential of marine invertebrates to climate change stressors and the methods that have been applied to this research, including quantitative genetics, laboratory selection studies and trans- and multigenerational experiments. Phenotypic plasticity is likely to contribute to population persistence providing time for genetic adaptation to occur. Transgenerational and epigenetic effects indicate that the environmental and physiological history of the parents can affect offspring performance. There is a need for long-term, multigenerational experiments to determine the influence of phenotypic plasticity, genetic variation and transgenerational effects on species' capacity to persist in a changing ocean. However, multigenerational studies are only practicable for short generation species. Consideration of multiple morphological and physiological traits, including changes in molecular processes (eg, DNA methylation) and long-term studies that facilitate acclimatization will be essential in making informed predictions of how the seascape and marine communities will be altered by climate change.

1. THE IMPACT OF CLIMATE CHANGE ON THE OCEANS

The emission of CO_2 and other greenhouse gases has enhanced the greenhouse effect, whereby atmospheric gases trap radiation from the sun and surface of the Earth. This is causing climate change, with an increase in both atmospheric temperature and sea surface temperature (SST) (IPCC, 2013). Since 1960, 90% of the excess heat in the atmosphere has been absorbed by the ocean and over the past century, SST has risen from 0.4°C to 0.8°C, with warming observed to depths of 6000 ft (Roemmich et al., 2015; Sabine et al., 2004). Coincidentally, thermal expansion and melting of glaciers due to warming has contributed to a rising sea level (IPCC, 2013). The Intergovernmental Panel on Climate Change (IPCC) predicts that the surface ocean temperatures will increase by 1.2–3.2°C by 2100 (Gattuso et al., 2015; Hobday and Lough, 2011; Howes et al., 2015; IPCC, 2013).

The oceans constitute an important sink for atmospheric CO_2, thereby strongly influencing the Earth's climate (Gattuso et al., 2015; IPCC, 2013). The oceans have absorbed around 40% of global anthropogenic CO_2 emissions (IPCC, 2013; Zeebe et al., 2008). In seawater, dissolved CO_2 forms carbonic acid and causes a decrease in carbonate ion concentration and an increase in bicarbonate ion concentration. This results in a release of hydrogen ions to maintain equilibrium, thus lowering pH, a phenomenon known as ‘ocean acidification’. Since the industrial revolution, the mean pH of ocean surface water has decreased by 0.1 pH units, corresponding to a 26% increase in hydrogen ion concentration (Rhein et al., 2013). Continued oceanic uptake of CO_2 will further reduce ocean pH (Caldeira and Wickett, 2005). By 2100, ocean pH is expected to drop by 0.14 to 0.4 units (Caldeira and Wickett, 2005; Gattuso et al., 2015; Howes et al., 2015; IPCC, 2013).

For marine ectotherms (cephalopods being a potential exception) (Melzner et al., 2009), two factors covary with CO_2-driven decrease in ocean pH: (1) hypercapnia, the increase in organism partial pressure of CO_2 (pCO_2), and (2) the decrease in saturation of calcium carbonate ($CaCO_3$). Hypercapnia is coupled to acidosis of cells, which can hinder metabolism, leading to impaired growth and reproduction (Melzner et al., 2009; Pörtner, 2008). Carbonate ions combine with the hydrogen ions to form bicarbonate thus decreasing the concentration of $CaCO_3$ in seawater. This reduces the availability of carbonate minerals required by calcifiers to build skeletons and shells (Guinotte and Fabry, 2008; Howes et al., 2015; Kerr, 2010).

The resulting changes in marine chemistry are even more complex in coastal ecosystems due to a multitude of drivers influencing pH including nutrient inputs, watershed processes and tidal exchange (Duarte et al., 2013). In addition, marine animals are exposed to many other anthropogenic stressors including decreased salinity, hypoxia and nutrient enrichment (Levin, 2003; Przeslawski et al., 2015). While these and other stressors are important to consider, assessment of the full range of stressors is beyond the scope of this review. Here, we focus on ocean warming and acidification, which are global stressors that pose serious threats to marine species. Thus, the aim of this review is to summarize literature on the adaptive potential of marine invertebrates and whether they show the ability to acclimatize or adapt to an ocean decreasing in pH and increasing in temperature. Methods to assess evolutionary potential of free spawning animals are considered, covering quantitative genetic designs, clonal studies, laboratory selection studies as well as trans- and multigenerational studies to provide a guide on the use of these approaches and to inform future experimental methods. Table 1 provides a glossary of key evolutionary biology and quantitative genetic terms included in this review.

Table 1 Glossary of Evolutionary Biology and Quantitative Genetic Terms

Term	**Definition**
Acclimation	A laboratory phenomenon where species adjust to experimental conditions without an adjustment in their genetics
Acclimatization	Similar to acclimation, however, the term used when the effect is induced by natural environmental changes
Adaptive evolution	Genetic change in a population over many generations to adjust the organism to its environment. It is maintained by natural selection
Additive genetic variation	Primary cause of resemblance between relatives and primary determinant of observable genetic properties of the population, and of the population response to selection
Allele	Alternative forms of a gene found at the same location on a chromosome
Broad-sense heritability	Broad-sense heritability of a trait describes the proportion of phenotypic variation due to genetic effects, and thus may also include dominance and epistasis effects
Dam	Female parent
Dominance	The connection between alleles in one gene where the effect of one allele on phenotype masks the contribution of the second allele
Epigenetics	Heritable modification of gene expression without change to DNA sequences. DNA methylation, modification of histones and noncoding RNA associated gene silencing are all systems that can initiate epigenetic change
Epistasis	Interactions within or between genes
Evolutionary rescue	The genetic adaptation of a population allowing persistence through environmentally induced effects that would have otherwise caused extinction
Fitness	The potential of a certain genotype to pass on genes to future generations that influence reproductive success

Table 1 Glossary of Evolutionary Biology and Quantitative Genetic Terms—cont'd

Term	**Definition**
Genetic assimilation	The process where phenotypes induced by an environmental signal become genetically fixed via natural selection (ie, the environmental signal is no longer required for expression of that phenotype)
Genetic correlation	The proportion of variance that two genetic traits share
Genetic rescue	Increased population fitness and genetic diversity through immigration of new alleles
Genotype × Environment (G × E) interactions	The differing responses of individual genotypes under changes in the environment
Heritability	The proportion of observed differences of a trait among individuals due to genetic differences
Narrow-sense heritability	The proportion of genetic variation that is due to additive genetic effects only and describes the degree of resemblance between relatives
Nonadditive genetic variation	The proportion of phenotypic variance that is due to epistatic interactions and dominance deviations
North Carolina II	A breeding design involving individual mating of N_{sires} and N_{dams} to allow partitioning of the phenotypic variance of offspring of known relatedness into genetic and environmental components
Phenotypic plasticity	The ability of an organism of one genotype to produce more than one phenotype when exposed to different environments. Plasticity can be adaptive (promotes persistence in new environment) or nonadaptive (response is away from favoured optimum)
Quantitative genetics	The study of the effects that heredity and environment have on traits that can be quantitatively measured
Reaction norm	This is also known as interaction plot, and shows the pattern of phenotypic expression of specific genotypes over certain environments
Selection	Where the environment or genetics determine which types of organism succeed

Continued

Table 1 Glossary of Evolutionary Biology and Quantitative Genetic Terms—cont'd

Term	Definition
Selective breeding	Also known as artificial selection, this is the process whereby animals and/or plants are bred for particular traits
Sire	Male parent
Transgenerational effects	Effects on offspring phenotype and patterns of gene expression that are passed from one generation to the next that cannot be explained by changes to the DNA sequence
Transgenerational plasticity	The transmission of information from one generation to the next resulting in an alteration of traits without an alteration to DNA. Transgenerational effects can be adaptive, resulting in preadapted offspring that exhibit traits associated with increased fitness in environmental conditions that were experienced by their parents

1.1 Early Developmental Stages of Marine Invertebrates and Ocean Climate Change Stressors

The life cycle of many marine invertebrates involves broadcast spawning of eggs and sperm, and fertilization in the water column. Spawning often takes place synchronously, usually triggered by water temperature, photoperiod, lunar cycle, phytoplankton, pheromones or other environmental cues. Invertebrates such as corals and sea urchins have developed mechanisms to increase the chances of fertilization in mass spawning events (Babcock et al., 1986), and release of chemoattractive molecules to guide sperm to eggs (Miller, 1985).

Many marine invertebrates have a characteristic planktonic larval stage. Notably, the planktonic larvae of many echinoderms and molluscs calcify. Such calcifying larvae are considered particularly vulnerable to ocean acidification, due to reduced mineral saturation and energetic considerations (Kroeker et al., 2013; Przeslawski et al., 2015). Marine larvae are important for species dispersal and may spend hours to months in the water column before metamorphosing into juveniles. These early developmental stages are the life history stages most sensitive to stressors and are key for assessing species vulnerability to ocean climate change (Pechenik, 1989; Thorson, 1950). Thus, marine invertebrate embryos and larvae are often used as a bioassay system for monitoring water quality and environmental pollutants (Byrne, 2011, 2012; Carr et al., 2006).

Because marine invertebrates experience exposure to simultaneous ocean climate change stressors, the effects of these stressors are likely to be interactive. Moreover, since the combined effects of multiple stressors are often greater than the individual effects of a stressor, research focusing on multiple stressors is required to represent real life scenarios (Byrne, 2012; Munday et al., 2013; Przeslawski et al., 2015; Sunday et al., 2014). For example, Przeslawski et al. (2015) conducted a meta-analysis of the effects of multiple abiotic stressors on marine invertebrates in early developmental stages and found that synergistic stressor interactions were the most common (65% of interactions). In addition, larvae were generally more vulnerable than embryos to increased temperature and acidification. Ocean acidification was found to be a greater stressor for invertebrates with calcifying larvae (Przeslawski et al., 2015).

2. THE POTENTIAL TO PERSIST IN THE FACE OF OCEAN CLIMATE CHANGE—ACCLIMATIZATION AND ADAPTATION

Environmental stressors, including those associated with climate change, are a significant evolutionary force that influences the shape of marine communities through selection (Hoffmann and Merilä, 1999). The adaptive capacity of marine species involves a mixture of organism plasticity, shifts in species range and genetic evolution (Chevin et al., 2010; Garcia Molinos et al., 2015). The pace of adaptation to ocean climate change will be greatly influenced by stress tolerance, dispersal ability, the latitudinal range the species inhabits and potential for genetic change (Bernhardt and Leslie, 2013; Williams et al., 2008). The four main population responses to global climate change stressors are (1) acclimatization, (2) shifts in distribution, (3) microevolution/adaptation, and (4) extinction (Hoffmann and Parsons, 1991).

Acclimatization allows species adjustment, within an individual's lifetime, to a new or changing environment. It involves phenotypic plasticity, wherein changes in physiology as a result of environmental conditions can generate a range of phenotypes from a single genotype (Chown et al., 2010; Sultan, 2007; Whitman and Agrawal, 2009). Thus, phenotypic plasticity provides potential short-term resilience to climate change stressors (a resilience that can potentially be conveyed further through transgenerational, epigenetic effects of these stressors, as discussed later). It is possible that such plastic resilience is passed on to offspring, a form of developmental plasticity through the influence of adult environment on gamete quality (Ghalambor et al., 2007). This 'gamete imprinting', may be particularly important with respect to protective factors present in the egg (eg, heat shock proteins) (see Hamdoun and Epel, 2007). For instance, in the Antarctic sea urchin, *Sterechinus neumayeri*, eggs of females from a polluted field site (near McMurdo Station) had greater levels of antioxidants providing the embryos with a greater ability to reduce oxidative damage to lipids than those of females from a relatively pristine site (Cape Evans) (Lister et al., 2015).

Adaptation, or microevolution, occurs over many generations and is a heritable, genetic change in response to environmental selection (Hoffmann and Merilä, 1999; Hoffmann and Parsons, 1991). Adaptation involves a change in gene frequency within a population, with natural selection playing a primary role (Hoffmann and Parsons, 1991). For research on the effects of climate change stressors on marine invertebrates species, it is important to be able to determine whether responses are genetic or phenotypic (Gienapp et al., 2008).

Overall, relatively few studies consider adaptive capacity of marine species to climate change (Merilä and Hendry, 2014). Thus far, most climate change stressor studies have involved placing the life stages of marine species directly into future scenarios. Although this approach provides some insight into the stress tolerance of species, it represents a 'future shock' approach and may overestimate the sensitivity to stressors (Byrne, 2012; Dupont et al., 2013). Experiments need to go beyond the limited life stage and short-term approaches, to complete the life cycle of species and, where possible, incorporate acclimatization to a new environment (see Carey et al., 2016). These are important considerations as climate change is much more gradual than in typical experimental conditions (Gaylord et al., 2014; Munday et al., 2013; Somero, 2012; Stillman and Paganini, 2015), as it is possible that some animals (eg, copepods, polychaetes) can evolve on rapid ecological timescales in tens of generations or even fewer (Carroll et al., 2007).

2.1 Acclimatization

Marine animals, such as those that reside in the intertidal, may be adapted to tolerate fluctuating environments (Byrne, 2011; Melzner et al., 2009; Sanford and Kelly, 2011). Intertidal habitats can fluctuate more than 0.5 pH units daily (Duarte et al., 2013; Wootton et al., 2008), a phenomenon also noted for coral reefs during day–night cycles (Birkeland et al., 2008). Some populations of the dwarf cushion star, *Parvulastra exigua*, are known to experience pH levels from

7.54 to 8.91, and temperatures from 10°C to 24°C across a 24-h cycle in the tide pools it inhabits (Nguyen and Byrne, 2014). Juveniles from these populations appeared to be resilient to conditions, including ocean warming and acidification, similar to those that are expected to result from future climate change. Adults also showed high metabolic resilience to ocean warming and acidification (McElroy et al., 2012). On the other hand, the California mussel, *Mytilus californianus,* experiences fluctuations in pH due to seasonal upwelling but is less tolerant to acidification than its congener, the Mediterranean mussel, *Mytilus galloprovincialis*, which occurs in a more stable pH environment (Waldbusser et al., 2015).

Although many shallow water and intertidal species inhabit environments where temperature and pH can fluctuate markedly, laboratory studies rarely incorporate fluctuating conditions. One study that compared the response of the coralline macroalgae *Arthrocardia corymbosa*, to a constant low-pH treatment and to a treatment that incorporated natural diurnal pH fluctuations, found that growth was reduced in low pH, and further reduced when the low-pH treatment was fluctuating (Cornwall et al., 2013). However, fluctuating pH conditions have also been found to reduce the negative effect of acidification on corals (Dufault et al., 2012).

2.1.1 Acclimatization and Thermal Tolerance Limits

Species with broad latitudinal distributions across thermal regimes may have the capacity to persist in warming oceans (Bradshaw and Holzapfel, 2001; Sunday et al., 2015). It is often found that progeny of individuals from cooler climates are less thermotolerant than those from the warmer regions of the range; likely due to adult thermal acclimatization (Byrne et al., 2010; Visser, 2008; Zippay and Hofmann, 2010). For the sea urchin *Heliocidaris erythrogramma*, northern (warmer) populations show significantly higher warm thermal tolerance than southern (cooler) populations, providing the possibility that these populations could persist through poleward migration of thermotolerant propagules with southward flow of the East Australian Current (Byrne et al., 2010). Similar possibilities for poleward migration could exist for the common periwinkle, *Littorina littorea*, and the blue mussel, *Mytilus edulis*, where warmer populations have a higher thermal tolerance than their cold adapted counterparts (Jones et al., 2009; Sorte et al., 2011). Geographic range shifts in relation to climate change have been reported globally (Sunday et al., 2015) and are creating novel communities as well as novel species interactions (Burrows et al., 2014; Sunday et al., 2015).

Temperature acclimatization capacities differ greatly among marine invertebrates, with thermal tolerance limits set by varying physiological constraints (Somero, 2010). Some organisms can alter their physiology in response to various environmental factors (without genetic change), thereby reducing their sensitivity to temperature change (Chevin et al., 2010; Hoffmann and Sgrò, 2011; Seebacher et al., 2014; Stillman and Paganini, 2015). Although physiological acclimatization to a changing climate is a feature of many species, a recent meta-analysis, which collated data for ectothermic animals in response to increased temperature, showed that physiological rates have increased ~20% in the past 20 years (Seebacher et al., 2014). Differential metabolic rates, heart rates, enzyme activities and locomotor performance may explain differences in thermal acclimatization potential between species (Seebacher et al., 2014). It is not known whether this increase in physiological rates is detrimental, having the potential to compromise normal physiological functioning. However, fully acclimated adult sea urchins (*H. erythrogramma*) living in a new environment of increased temperature and acidification, showed an increase in basal metabolism in comparison to resident controls, with additive negative effects of the two stressors (Carey et al., 2016).

Phenotypic plasticity of many marine invertebrates has been investigated using laboratory studies on thermal tolerance limits and acute heat stress tests because temperature is a key factor determining the biogeography and distribution of marine species (Monaco and Helmuth, 2011; Somero, 2010; Sunday et al., 2014; Terblanche et al., 2011; Tomanek, 2010). For example, large thermal envelopes for development have allowed expansion of invasive species in a warming ocean, as shown for the sea urchin *Centrostephanus rodgersii*, which has a 9°C thermal envelope (13–22°C) for development (Ling et al., 2009). This influenced expansion of this species over 1000 km in ~60 years (Ling, 2008). The lower thermal limit for successful development of *C. rodgersii* corresponds to the maximum winter temperature in Tasmania, thus allowing local populations to reproduce (Hardy et al., 2013; Ling et al., 2009). Similarly, for *C. rodgersii* in New Zealand, the thermal window for early development is likely to contribute to its current distribution, where the current southern limit of distribution coincides with the lower limit of their larval thermal window (Pecorino et al., 2013).

Although species may display broad developmental thermal envelopes, it does not necessarily mean that such envelopes are reflected in their latitudinal distributions (Garcia Molinos et al., 2015; Hardy et al., 2013). The tropical echinoid *Arachnoides placenta*, displays a broader envelope (17–31°C) than does *C. rodgersii* (13–22°C), but has not expanded its distribution, likely due to limited habitat (Hardy et al., 2013). For both species, potential future warming of their habitat could lead to contractions at their warm range edge as they are currently living near the upper thermal tolerance limits (Hardy et al., 2013).

Many marine species appear to be operating at the edge of their thermal tolerance (Sunday et al., 2014), and further acclimatization to warming may be limited, especially for some polar species (Peck, 2015; Peck et al., 2009). The exception may be the asteroid *Odontaster validus*, an ecologically dominant species that is also one of the most thermotolerant of Antarctic marine species studied to date and so may be resilient to habitat warming (Peck et al., 2008). However, a recent laboratory study of the porcelain crab, *Petrolisthes cinctipes,* indicated that in the short term, increased tolerance to warmer temperatures is beneficial, but in the long term the effects are detrimental due to a reduction in overall energy (Paganini et al., 2014).

Recent work demonstrates that it is important to assess the thermal tolerance of adults and progeny with respect to other traits such as metabolic performance, swimming ability and sublethal responses (eg, reproduction and growth) to more fully understand species' vulnerability, and to forecast individual responses to ocean change (Chan et al., 2015; Chown et al., 2010; Dawson et al., 2011; Francis Pan et al., 2015; Magozzi and Calosi, 2015; Stumpp et al., 2011; Sunday et al., 2015). In response to ocean warming, based on climate velocity trajectories and species' thermal tolerance, current biodiversity is likely to be redistributed according to the ability of marine ectotherms to adapt to their thermal niche, dependent on suitable colonization conditions (Burrows et al., 2014; Garcia Molinos et al., 2015; Sunday et al., 2015).

Because marine organisms are typically subject to multiple stressors, which may be in combination with thermal stress, the addition of a second stressor (eg, ocean acidification) may reduce thermal tolerance breadth (Pörtner, 2008, 2010). This has been observed in larvae of the sea urchin *Strongylocentrotus purpuratus*, where increased temperature and low pH had additive effects that exceeded thresholds for optimal physiological performance as revealed by significant reductions in larval metabolism and downregulation of histone encoding genes (Padilla-Gamino et al., 2013). Embryos of *S. neumayeri* reared in control conditions were able to survive heat shocks up to +20°C, 5°C higher than those reared in low-pH conditions (Kapsenberg and Hofmann, 2014).

2.1.2 Phenotypic Plasticity and Genetic Assimilation

When phenotypes induced by environmental conditions become genetically fixed through natural selection, even when the environmental signal is no longer required for expression of that phenotype, genetic assimilation has occurred in the population (Collins et al., 2013; Pigliucci et al., 2006). Genetic assimilation can facilitate phenotypic evolution and can thus alter natural selection (Pigliucci et al., 2006). However, it is often contested whether phenotypic plasticity facilitates or hinders genetic evolution (Chevin et al., 2010; Merilä, 2015). A recent study on Trinidadian guppies, *Poecilia reticulata*, provides evidence that adaptive phenotypic plasticity can weaken the strength of directional selection, which in turn reduces the rate of genetic adaptation (Ghalambor et al., 2015). However, the study also found that 89% of the genes expressed changed in the opposite direction to that of phenotypic plasticity. This inverse relationship may facilitate evolution by increasing directional selection (Ghalambor et al., 2015).

Thus, in the short term, acclimatization may allow adjustment to changing conditions in some species and may provide the time required for genetic adaptation to occur (Chevin et al., 2010). However, plasticity has limits in its potential to buffer marine ectotherms to increased temperature and acidification (Gunderson and Stillman, 2015). Therefore in the long term, adaptation is required for population persistence (Hoffmann and Parsons, 1991).

2.2 Adaptation

The ability to adapt to future changes in environmental conditions depends on the existence of additive genetic variances within populations, the proportion of genetic variation that responds to natural selection (Billington and Pelham, 1991). Selection will favour individuals with more advantageous traits where the genetic basis of these phenotypes will become more common in a population, eventually resulting in macroevolution and the dominance of the favourable genotype (Gassmann et al., 2009; Hoffmann and Parsons, 1991). Types of genetic variance include additive and nonadditive, with the latter being interactions between parental haplotypes. Additive genetic variance is considered to be the intrinsic genetic quality of the male and female parent (Neff and Pitcher, 2005). Natural selection favours traits that facilitate success of subsequent generations. The potential to adapt to the pressures exerted by climate change depends upon the rate at which climate change stressors are being altered and the amount of additive genetic variation in fitness related traits within populations (Billington and Pelham, 1991).

If there is a selection gradient, traits are heritable, and if genetic variance is present in the population, adaptation to climate change stressors can proceed (Dam, 2013).

The rate of adaptation is influenced by generational turnover time with short-lived species, and those with fast generation times likely to show greater potential evolutionary adaption (Dam, 2013). For example, when exposed to low pH, the coccolithophore *Emiliania huxleyi*, showed a restoration in growth and calcification in selected clones after 500 asexual generations (Lohbeck et al., 2012). Similar results were observed for sexual reproduction in the copepod *Tisbe battagliai*, after three generations in low pH (Fitzer et al., 2012).

2.2.1 Evidence of Standing Genetic Variation

Standing genetic variation, may provide a reservoir of resilience to ocean change (Anttila et al., 2013; Hoffmann and Sgrò, 2011; Kelly et al., 2013; Pespeni et al., 2013a,b). For the Atlantic salmon, *Salmo salar*, high phenotypic variation between families and great similarity between siblings indicates the presence of standing genetic variation in the response to increased temperature, providing increased resilience to ocean warming (Anttila et al., 2013). Garfield et al. (2013) found extensive variation in gene expression in the gene regulatory network for the sea urchin *S. purpuratus*, and this was associated with measurable variation in larval skeleton morphology. As the expression of most genes were attributed to significant paternal effects, this variation is likely to be heritable and shows that the larval skeleton is a trait that can be targeted by natural selection (Garfield et al., 2013).

Studies of local adaptation can provide important information on the potential for natural selection, giving insight into the ecological and genetic factors that influence evolution (Kawecki and Ebert, 2004). Latitudinal temperature gradients appear to have generated local genetic adaptation in *S. purpuratus* along the coast of North America, despite having an open population with a recruitment regime dependent on larvae. Larvae generated from the gametes of adults from six populations of *S. purpuratus* spanning regions of different temperature showed differences in gene regulation related to biomineralization and ion transport (Pespeni et al., 2013a). Pespeni et al. (2013b) cultured larvae from seven populations of *S. purpuratus* inhabiting the US west coast. Adults spawned in the laboratory were the progeny of adults that had been collected from different pH environments (due to variable upwelling conditions along the coast). Fertilized embryos were cultured in a current global mean $p\text{CO}_2$ (partial pressure of

CO_2 ~400 µatm) and in a fossil-fuel intensive projection of future pCO_2 (~900 µatm). Although there was little observable difference in performance of larvae between low pH and control conditions, larvae from different populations showed significant differences in over 40 functional groups of proteins, including genes for lipid metabolism and biomineralization (Pespeni et al., 2013b).

Populations of the coral *Acropora hyacinthus*, that live in naturally high-temperature environments, are more resistant to bleaching, which has been suggested to be due to a reservoir of alleles that allow preadaptation to high temperature (Bay and Palumbi, 2014; Palumbi et al., 2014). Furthermore, constitutive frontloading of transcripts related to heat shock proteins and antioxidant enzymes enable corals to maintain physiological homeostasis during periods of temperature stress (Barshis et al., 2013). In addition, an increase in photoprotective mechanisms reducing symbiont loss was observed for *Acropora aspera* that were exposed to 31°C (4°C above ambient) prior to exposure to 34°C, to simulate a bleaching event (Middlebrook et al., 2008).

These examples demonstrate the potential capacity of some species for rapid evolution in response to ocean acidification and warming, due to standing genetic variation present in current populations.

2.2.2 Assisted Evolution

Assisted evolution is defined as the process whereby human intervention is used to accelerate the rate of naturally occurring evolutionary processes. This can be done through deliberate translocation of species to refuge habitat where adaptation to a new regime is facilitated, and by genetic rescue, whereby the deliberate introduction of new alleles into a population is used to restore growth and facilitate population resilience to stressors (Whiteley et al., 2015).

Assisted evolution has recently been identified as a possible method of restoring coral growth through identification of corals with enhanced stress tolerance (Van Oppen et al., 2015). Coral nurseries are used to grow coral to a size that allows them to survive transplantation and seeding of degraded reefs (Amar and Rinkevich, 2007; Guest et al., 2014). This idea can be expanded through selection of resistant zooxanthella symbionts. In assisted evolution studies these symbionts are subjected to ocean change stressors in the laboratory to identify strains with enhanced tolerance (Van Oppen et al., 2015). Larval and juvenile corals can then be inoculated with the stress-tolerant symbionts.

Genetic improvement of many plants and animals has been utilized for many years, and could help augment the capacity of corals and other ecologically and economically significant species to endure a changing climate (Van Oppen et al., 2015). When selectively bred lines of the Sydney rock oyster, *Saccostrea glomerata*, were exposed to low pH, the disease resistant lines were more resilient with respect to shell growth in comparison to wild oysters, showing the importance of the aquaculture industry in identifying resilient subsets of marine species (Parker et al., 2011). When the offspring of these oysters maintained under low pH were outplanted into ambient conditions until reproductive maturity, positive carry over effects were still evident in the F2 generation. These results demonstrate the potential application of assisted evolution to generate resilient genotypes using laboratory selection and subsequently outplanting progeny (Parker et al., 2015).

2.2.2.1 Evolutionary Rescue

Evolutionary rescue occurs when a population has been able to genetically adapt in the face of environmental change, either through assisted or natural evolution (Carlson et al., 2014; Gonzalez et al., 2013; Whiteley et al., 2015). The potential for evolutionary rescue depends on population size, organism life span and the amount of genetic variance present for the trait under selection (Bell and Gonzalez, 2009; Hoffmann and Sgrò, 2011; Willi et al., 2006). Determining the existence of genetic variation in populations will help to determine whether evolutionary rescue is possible in the context of ocean warming and acidification.

Carter et al. (2013) observed that some larvae and juvenile porcelain crabs, *P. cinctipes*, had increased tolerance to decreased pH. In that study, enhanced acid–base regulation in a resilient subset of crabs allowed a greater compensation of extracellular pH, and prevented a decrease in metabolism, a phenomenon that has been observed in other ectotherms in response to decreased pH (Carter et al., 2013). This variable response across a population of crabs suggests potential for certain individuals to adapt to ocean acidification.

Studies that track specific genotypes' performance across environmental conditions have shown genetic variation in response to ocean acidification (Kelly et al., 2013; Sunday et al., 2011), ocean warming (Pistevos et al., 2011), as well as to the combination of warming and acidification (Foo et al., 2012, 2014). For sea urchins, bryozoans and mussel species investigated in these studies, the presence of genetic variance in response to the stressor of interest suggests the potential for evolutionary rescue of these populations in the context of a changing climate.

3. EXPERIMENTAL APPROACHES TO ASSESS EVOLUTIONARY POTENTIAL

To assess whether a population can respond to acidification and warming, studies have investigated the magnitude of genetic variance and/or presence of tolerant genotypes in environments that differ in stressor levels (see Tables 2–4). Experimental designs have been used to replicate genotypes in different ways including as full-sib or half-sib families, or clones. Performance of the different genotypes has been assessed across various environmental conditions allowing an interaction between genotype and the stressor to be detected with these responses visualized through reaction norms (Fig. 1). These interactions are indicative of genetic variation in stress tolerance. The heritability of stress tolerance can also be estimated based on these types of experimental quantitative genetics (Shaw and Etterson, 2012).

3.1 Reaction Norms and Visualization of Genotype by Environment Interactions

When phenotypic variation occurs as a result of exposure to different environmental conditions, this is indicative of interactions between genes and the environment (G × E interaction; Neff and Pitcher, 2005). Reaction norms show the response of a specific genotype across a range of environments and allow visualization of G × E interactions (Lynch and Walsh, 1998). Four main environmental response patterns (reaction norms) can occur (see Fig. 1A–D): (1) different genotypes display a similar response to a range of environments due to previously strong selection; (2) genotypes display parallel responses (these examples do not show evidence of genetic variation); (3) nonparallel reaction norms or trait expression across environments with genotypes responding similarly in some environments but differently in others, affecting selective outcomes and (4) the rank order of the genotypes for a trait varies depending on the environment (Neff and Pitcher, 2005; Sultan, 2007). The latter two response patterns, which are more common, are indicative of G × E interactions. Thus, a G × E interaction can be summarized as a genotype that performs well in one environment, but not as well in a second environment (Eisen and Saxton, 1983).

Table 2 Studies of Marine Species That Have Used the North Carolina II Design to Test for Within-Population Genetic Variation in Tolerance to Ocean Change and Other Anthropogenic Stressors

Species	Stressor/Trait	Experimental Design	Fertilization Conditions	Results	References
Single stressor studies					
Hormosira banksii (brown algae)	Temperature/ growth, photosynthesis	NCII design, 3 sires × 3 dams × temperature, fully crossed	Crosses were fertilized and left for an hour in control conditions to let phototactic zygotes settle and then transferred to treatments	Genetic variation in thermal sensitivity	Clark et al. (2013)
Strongylocentrotus franciscanus (the red sea urchin) and *Mytilus trossulus* (mussel)	pH/growth	NCII design, sire × dam × pH, fully crossed (*M. trossulus*, 4 dams and 10 sires; *S. franciscanus*, 10 dams and 10 sires)	Crosses were fertilized in control conditions and then transferred to treatments	*Strongylocentrotus franciscanus* showed greater genetic variation for larval size in response to ocean acidification than *M. trossulus*	Sunday et al. (2011)
Strongylocentrotus purpuratus (the purple sea urchin)	pH/larval size	Modified NCII, 2 sires × 4 dams (where 1 male and 2 dams of each cross were from different sites)	Not stated	Incorporating heritability/ adaptation into modelling showed that the low pH driven decrease in population growth rate is up to 50% smaller than that predicted by the 'no-adaptation' scenario	Kelly et al. (2013)

Continued

Table 2 Studies of Marine Species That Have Used the North Carolina II Design to Test for Within-Population Genetic Variation in Tolerance to Ocean Change and Other Anthropogenic Stressors—cont'd

Species	Stressor/Trait	Experimental Design	Fertilization Conditions	Results	References
Heliocidaris erythrogramma armigera (sea urchin)	Temperature/larval hatching success	NCII design, 3 sires × 3 dams × temperature, fully crossed	Crosses were fertilized in control conditions where only fertilized eggs were transferred to treatments	Hatching success was reduced at higher temperatures, however analyses revealed significant additive genetic variance and G × E interactions underlying hatching success	Lymbery and Evans (2013)
Styela plicata (tunicate)	Copper/hatching success	NCII design, 3 sires × 3 dams ×copper concentration, fully crossed	Fertilized in control conditions and then transferred to treatments	Significant G × E interactions in hatching success across copper concentrations	Galletly et al. (2007)
Galeolaria caespitosa (polychaete)	Temperature/survival	NCII design, 2 sires × 2 dams, fully crossed	Fertilized in control conditions and then transferred to treatments after 2 h	Significant sire × temperature interactions with correlated responses across all thermal environments	Chirgwin et al. (2015)
Multistressor studies					
Centrostephanus rodgersii (sea urchin)	Temperature, pH/early development	NCII design, 3 dams × 3 sires × temperature × pH, fully crossed	Fertilized in treatments	Significant sire × stressor interactions indicate adaptive potential	Foo et al. (2012)
Pseudoboletia indiana (sea urchin)	Temperature, pH/early development	NCII design, 2 dams × 4 sires × temperature × pH, fully crossed	Fertilized in treatments	Significant sire × stressor interactions, increased temperature alleviated effects of low pH	Foo et al. (2014)

The stressors tested and biotic trait scored, experimental design, fertilization conditions and outcome are indicated. Most studies examine only one stressor and fertilize in control conditions.

Table 3 Studies of Marine Species That Have Used Clones to Test for Within-Population Genetic Variation in Tolerance to Ocean Change Stressors

Species	Stressor/Trait	Experimental Design	Results	References
Single stressor studies				
Zostera marina (seagrass)	Temperature/growth rate, survival	Field experiment using genotyping to identify different clones	Increasing genotypic diversity of seagrass communities helped maintain growth and survival even with exposure to high temperature	Reusch et al. (2005)
Zostera marina (seagrass)	Temperature/growth	Clone diversity × temperature	Positive effect of genotypic diversity on seagrass shoot densities in high temperature	Ehlers et al. (2008)
Acropora millepora (coral)	Temperature/ photosynthesis, gene expression, growth	Among clonal lineages, with four pairs of branches from 20 colonies	Coral symbionts possessed a much higher potential for thermal stress adaptation than their coral animal host	Császár et al. (2010)
Multistressor studies				
Celleporella hyalina (bryozoan)	Temperature, pH/ growth, reproduction	Four colonies (genotype) cut into 25 fragments (clones) and exposed to temperature × pH treatments	Genetic variation in response to low pH and high temperature was documented	Pistevos et al. (2011)
Celleporaria nodulosa (bryozoan)	Temperature, pH/ growth	Seven colonies cut into 18 fragments and exposed to temperature × pH treatments in Austral summer and in Austral winter	Seasonal differences were reported. In winter, low pH decreased growth. In summer, high temperature decreased growth of bryozoan colonies	Durrant et al. (2013)

The stressors tested and biotic trait scored, experimental design and outcome are indicated. Studies are separated into those that examine either single or multiple stressors.

Table 4 Studies of Marine Species That Have Used Selection Experiments with Short Generation Species to Test for Adaptation to Ocean Change Stressors

Species	Stressor/Trait	Experimental Design	Results	References
Scottolana canadensis (copepod)	Temperature/ growth	Northern (colder) and southern (warmer) populations reared in different temperature scenarios over several generations	Northern populations locally adapted to grow in lower temperatures	Lonsdale and Levinton (1985)
Acartia tsuensis (copepod)	pH/survival	The copepods were grown in low pH over two generations	No effect of low pH in copepods, with first and second generations developing from eggs to adults normally	Kurihara and Ishimatsu (2008)
Tisbe battagliai (copepod)	pH/naupliar production, growth	The copepods were raised in low-pH conditions for four generations	Copepods reallocated energy resources, inhibiting somatic growth	Fitzer et al. (2012)
Gephyrocapsa oceanica (coccolithophorid)	pH/growth rate, carbon fixation	The coccolithophores were exposed to low pH over 670 generations	Selected coccolithophores were adapted to low-pH conditions	Jin et al. (2013)
Tigriopus californicus (isopod)	Temperature/ survival	30 Different lines exposed over 10 generations to increased temperature	Low adaptation potential to increased temperature	Kelly et al. (2011)
Thalassiosira pseudonana (diatom)	pH/ photosynthesis	Diatoms were exposed to low-pH conditions over 100 generations	No evidence of genetic variation in low-pH conditions	Crawfurd et al. (2011)

Emiliania huxleyi (coccolithophore)	pH/growth, calcification	Exposed populations of clones to low pH and assessed growth over 500 asexual generations	Growth and calcification in selected clones raised in low pH was mostly restored	Lohbeck et al. (2012, 2014)
Daphnia pulex (crustacean)	Temperature, salinity/metabolism	*Daphnia* were raised for six generations in various temperature and salinity treatments	The effects of temperature and salinity were reduced with each generation grown in treatment conditions	Chen and Stillman (2012)
Calanus finmarchicus (copepod)	pH/food availability	The copepods were exposed to low pH for two generations under limited food availability	The delay in developmental rate observed in low pH in F1 disappeared in the F2 offspring	Pedersen et al. (2014)

The stressors tested and biotic trait scored, experimental design and outcome are indicated.

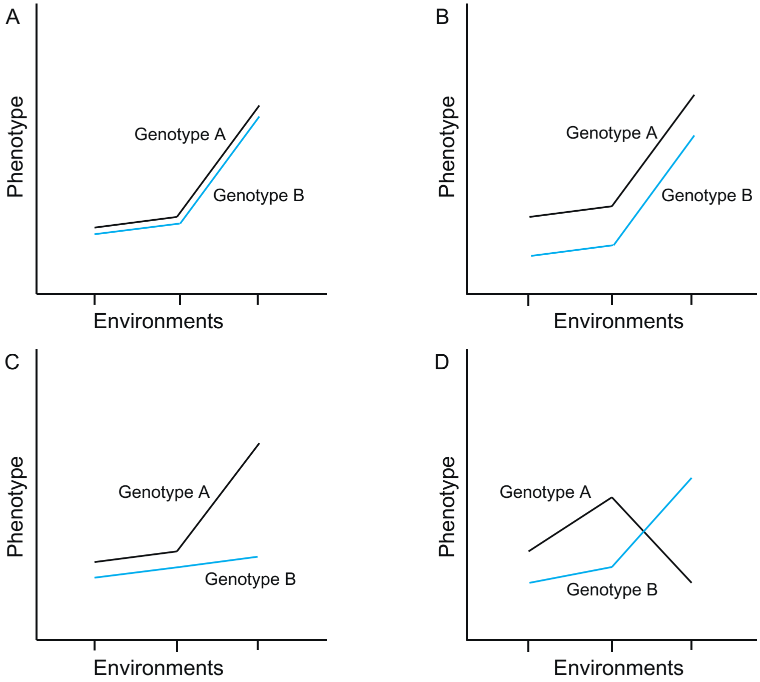

Fig. 1 The pattern of phenotypes produced by given genotypes under different environmental conditions (reaction norms). The variation in the fitness of a genotype and the expressed phenotype across multiple environments is due to genetic effects, environmental effects and genetic × environmental effects (G × E). Within a population, genotypes can show (A) almost identical responses across a range of environments, or (B) different responses consistently across environments. When the genotypic difference varies from one environment to another (nonparallel reaction norms), this is indicative of G × E interactions and is shown by a difference in the genotype's magnitude of response to environment by (C) expression of different genotypes only in some environments or (D) the rank order of the genotype varies depending on environment (ie, there is a G × E effect with a change in the fitness rank of the two genotypes), which can promote selective diversification among distinct environments.

3.2 Use of Quantitative Genetic Designs with Free Spawning Marine Invertebrates

To determine evolutionary potential, the additive and nonadditive components of genetic variance have to be estimated. Quantitative breeding designs, such as the North Carolina II (NCII), allow these variance components to be determined (Lynch and Walsh, 1998). The NCII involves mating a set of N_S sires with N_D dams in all combinations generating $N_S \times N_D$ families or genotypes, thus each family has half sibling relationships through the use of common males or females. This breeding design allows genetic effects to be detected because it examines all possible crosses between individuals and allows variance of a population among relatives of known relatedness to be partitioned into additive, maternal, interactive and environmental components (Lynch and Walsh, 1998). Free spawning marine invertebrates provide an ideal model system for utilization of the NCII design because they provide a tractable model system that can be controlled, to quantify the contribution of heritable genetic variation to the overall phenotypic variation (Fig. 2) (Lynch and Walsh, 1998; Neff and Pitcher, 2005).

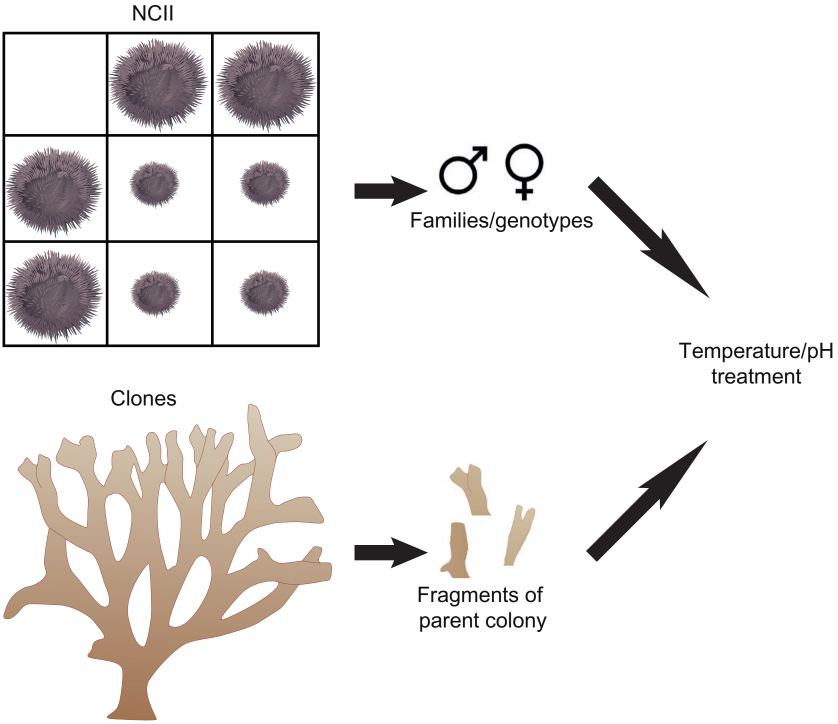

Fig. 2 The North Carolina II design with free spawning marine invertebrates. The design involves mating N_S sires with N_D dams in all combinations allowing genetic effects to be partitioned into additive, maternal, interactive and environmental components. The example on the top shows that fully crossing two dams with two sires result in four possible genotypes. For a tractable and robust design, this needs to be repeated in blocks to create large numbers of genotypes for analysis. Clonal studies replicate genotypes by using clones of colonial organisms such as corals and bryozoans. Clones of the same genotype can be placed across various treatments and performance contrasted. *Sea urchin and coral symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (https://ian.umces.edu/symbols/).*

Because the development of specific genotypes can be tracked using paired mating model systems, quantitative genetics and animal breeding designs, including the NCII, have been used for many years in agriculture and aquaculture to generate stress-tolerant animals and crops, and progeny most suited to a specific environment (Falconer and Mackay, 1996; Henning and Townsend, 2005; Lynch and Walsh, 1998). Selective breeding of Atlantic salmon has created family lines that are resistant to sea lice, a problem that is costly to the industry (Jones et al., 2002). Breeding for Pacific oysters, *Crassostrea gigas*, has selected for genetic improvement (eg, production of triploid offspring) and resistance to disease (Kube et al., 2011; Ward et al., 2000). Recently, pedigree inbred lines of *C. gigas* have shown potential for the redistribution of energy in response to ocean change stressors (Applebaum et al., 2014). Pedigree lines provide genotypes that can be retested, allowing nonadditive genetic components of phenotypic variance to be captured (Applebaum et al., 2014; Pace et al., 2006).

The NCII design has also been used to estimate the amount of variation in the size of the tropical abalone *Haliotis asinine*, attributable to additive genetic effects in selective breeding programmes (Lucas et al., 2006). Animal breeding design experiments with the ascidian *Styela plicata* show a difference in resistance to a range of copper concentrations in the progeny of different male–female crosses (Galletly et al., 2007), suggesting the presence of genetic mechanisms to adapt to different pollution levels.

The NCII design has recently been applied to marine species for assessment of their adaptive capacity to ocean climate change stressors. Thus far, there are only a few published studies using the gametes of free spawning invertebrates to investigate within population genetic variation for tolerance to climate change stressors (including temperature and/or acidification; see Table 2). Studies on sea urchins, mussels and macroalgae have found significant levels of variation among genotypes in their response to ocean warming and acidification, providing evidence for the potential to adapt (Clark et al., 2013; Foo et al., 2012, 2014; Kelly et al., 2013; Lymbery and Evans, 2013; Sunday et al., 2011). These studies have largely involved a single stressor (temperature: Chirgwin et al., 2015; Clark et al., 2013; Lymbery and Evans, 2013; acidification: Kelly et al., 2013; Sunday et al., 2011). Two recent studies investigating the response to concurrent warming and acidification (Foo et al., 2012, 2014), differ from other NCII experiments in that the male–female crosses were fertilized in treatments, not transferred to treatments after fertilization in control conditions.

Determination of paternal variance is a good way to estimate genetic quality and determine species' adaptive potential because the ability to adapt to future changes in the environment depends on the existence of additive genetic variance within populations and DNA is considered to be the only contribution from the father to offspring. A male possessing good genes will produce offspring with a higher fitness regardless of female genotype (Neff and Pitcher, 2005). A significant interaction between sire and temperature or pH indicates the presence of existing genetic variation in the response to the stressors, while a significant interaction between dam and either of these stressors may be due to phenotypic (eg, environmental and egg nutrients) or genetic variation. Examples of reaction norms displaying genetic variation are shown in Fig. 3. Maternal effects are, of course, also important in population evolutionary dynamics as they impact the rate and direction of genetic change under selection (Rasanen and Kruuk, 2007). However, there are two maternal effects components: genetic and environmental. These two components have not been possible to isolate in quantitative genetic experiments (Rasanen and Kruuk, 2007). An interaction between sire and dam would indicate genetic variance due to nonadditive genetic effects, ie, the influence of the particular compatibility of the set of male and female gametes

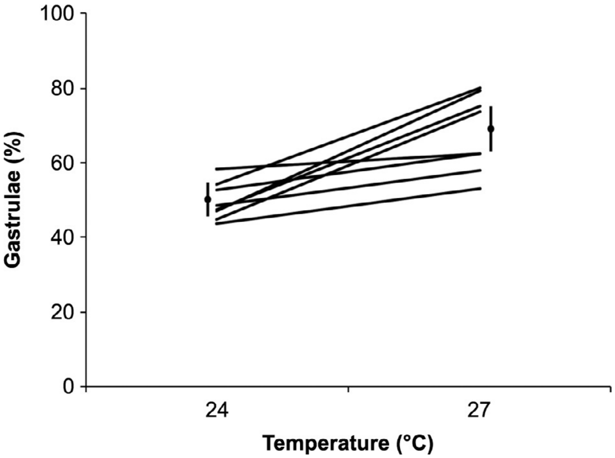

Fig. 3 Reaction norm showing the responses of the progeny of eight male genotypes to increased temperature. The reaction norms show the percentage of normal gastrulae in experimental temperatures pooled for pH. Lines represent the mean percentage of paternal half siblings with standard errors indicated ($n=8$). *From Foo, S.A., Dworjanyn, S.A., Khatkar, M. S. Poore, A.G.B., Byrne, M., 2014. Increased temperature, but not acidification, enhances fertilization and development in a tropical urchin: potential for adaptation to a tropicalized eastern Australia. Evol. Appl. 7, 1226–1237.*

(Falconer, 1989). Although these are nonheritable effects, investigation of pair compatibility is a feature of particular significance for many free spawning marine invertebrates (Evans and Marshall, 2005). Thus, it is important to conduct ocean change quantitative genetics experiments with progeny created by fertilization in the experimental environment. The performance of individual pairs can be assessed with the NCII design (see Fig. 4).

The source of variance attributed by the father may not be purely genetic. There is evidence that the environmental history of the sperm can alter sperm phenotype contributing to variation in sperm morphology, motility and longevity within an individual male and an individual ejaculate (Marshall, 2015). This difference in sperm phenotype may affect offspring phenotype. Within ejaculate differences in the sperm of the tunicate *S. plicata* has been shown to influence offspring fitness (Crean et al., 2012). Males were strip spawned and half the sperm was used to fertilize eggs immediately, while the other half was stored for an hour before use. Longer-lived sperm within a single ejaculate produced offspring of higher fitness compared to the sperm that was used immediately (Crean et al., 2012). In one study of the polychaete *Galeolaria gemineoa*, portions of sperm were kept in control (37 ppm) or low salinity (25 ppm) conditions. Larvae generated from sperm that experienced low salinity had lower developmental success in comparison to those from sperm that was kept in control conditions (Ritchie and Marshall, 2013). Furthermore, when sperm and larvae were kept in the same salinity range, offspring performance was higher than when sperm and larvae were kept at differing salinites, demonstrating significant covariance between sperm and offspring phenotype (Ritchie and Marshall, 2013). Although sperm (sire) effects are traditionally assumed to be purely genetic (Lynch and Walsh, 1998), recent studies indicate that sperm environment may also affect offspring phenotype (Crean and Bonduriansky, 2014). Thus, estimates of genetic variance based on paternal lines may not completely reflect paternal contributions, an important consideration in quantitative genetics studies (Crean and Bonduriansky, 2014).

Quantitative genetic designs are powerful tests, which may reveal hidden evolutionary capacity. Research exposing the polychaete *Galeolaria caespitosa*, to three temperatures 17°C, 21°C and 25°C), documented genetic variation in the species' response to the two lower temperatures but not to the highest temperature (Chirgwin et al., 2015). Although genetic variation was not present in response to all three temperatures, multivariate analyses revealed that *G. caespitosa* is likely to have high adaptive potential to all temperature

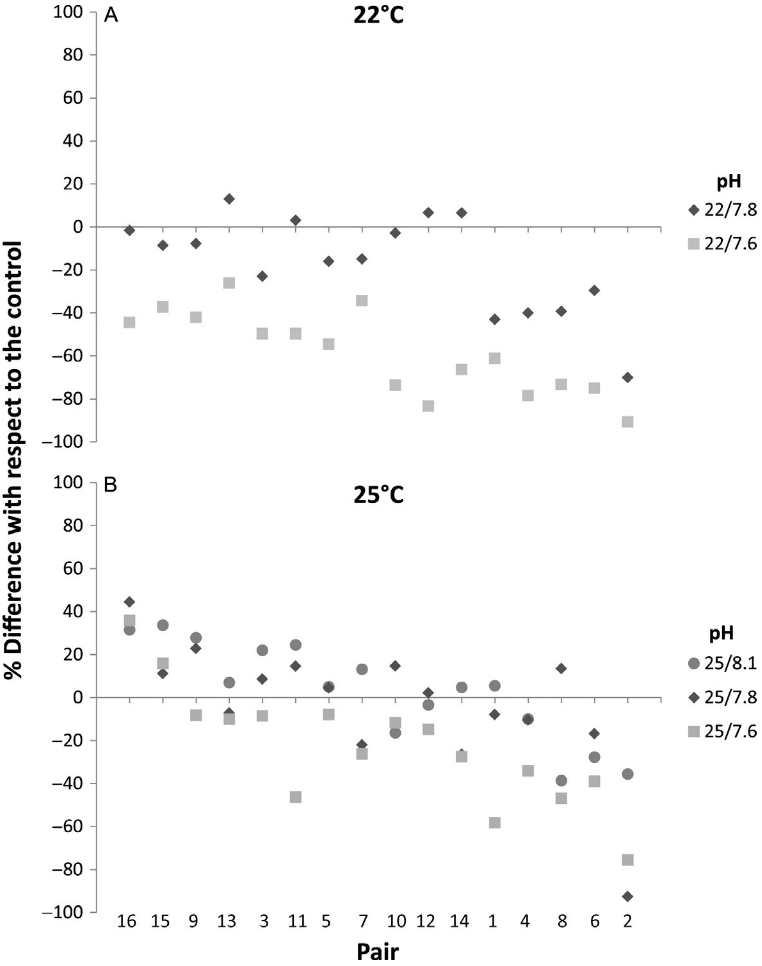

Fig. 4 The variation in fertilization success between 16 dam–sire pairs in a free spawning marine invertebrate with respect to the control treatment (22°C, pH 8.1) across five experimental treatments (2 temps × 3 pH). Mean fertilization success per genotype is displayed for the different pH levels across the control temperature (A) and increased temperature (B). Symbols above the line display higher fertilization success than the control, while symbols below the line represent fertilization success lower than the control. Pairs are ranked from the best to the worst performing from *left* to *right*. The difference in the performance between pair mating may be due to gamete compatibility as well as resistance to stress. *From Foo, S.A., Dworjanyn, S.A., Khatkar, M. S. Poore, A.G.B., Byrne, M., 2014. Increased temperature, but not acidification, enhances fertilization and development in a tropical urchin: potential for adaptation to a tropicalized eastern Australia. Evol. Appl. 7, 1226–1237.*

levels due to correlated responses to selection across all thermal environments (Chirgwin et al., 2015). However, because the matings in this study were conducted in control conditions with subsequent transfer of embryos to experimental temperature environments, the full extent of conveyance of thermal tolerance to the offspring is not known.

3.3 Clonal studies

Replication of genotypes without sourcing gametes for dam × sire crosses can be done with colonial organisms such as bryozoans and corals (see Fig. 2) (Császár et al., 2010; Durrant et al., 2013; Pistevos et al., 2011). In this approach, different colonies of the same species are used to represent different genotypes. A study by Durrant et al. (2013) compared the growth and survival rates of different colonies of the bryozoan *Celleporaria nodulosa* (collected from the same location), when exposed to elevated temperature and lowered pH treatments. Experiments were conducted in Austral winter (ambient SST 21.3°C) and summer (SST 25.4°C). Specimens of *C. nodulosa* were gravid during summer. Increased temperature and decreased pH reduced growth of all colonies with a large seasonal effect as elevated temperature significantly hindered growth in summer treatments, and lowered pH decreased growth in winter treatments (Durrant et al., 2013). However, there was no presence of G × E interactions as all genotypes (or clones) performed similarly in response to treatments in both seasons, indicating little adaptive potential within these populations under directional selection from climate change stressors. In contrast, another study using similar methods found that clones of the bryozoan *Celleporella hyalina* had contrasting responses to increasing temperature and decreasing pH, thus demonstrating the existence of genetic variation which may enable future adaptation to ocean change (see Table 3) (Pistevos et al., 2011), although seasonal affects were not considered.

3.4 Laboratory Selection Experiments with Short Generation Species

For taxa that have short generation times, laboratory selection experiments have been used to assess whether animals can adapt to environmental stressors over multiple generations. Taxa such as diatoms, phytoplankton and coccolithophores that can produce multiple generations in the order of hours to days, allow cultures of different genotypes to be followed over timescales during which populations can evolve (see Table 4; Fig. 5) (Collins et al., 2013; Dam, 2013; Kurihara and Ishimatsu, 2008; Stillman and

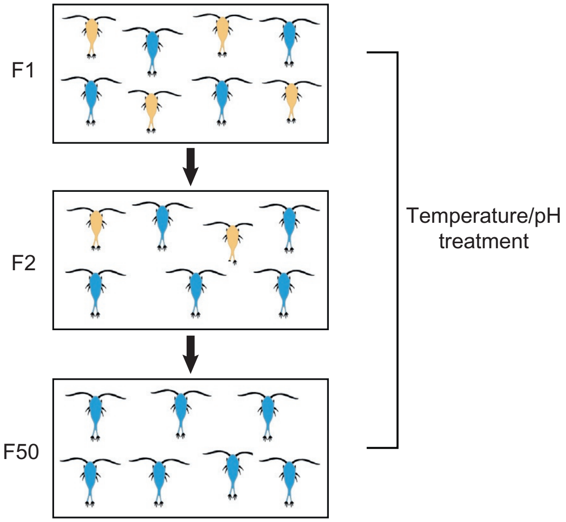

Fig. 5 Laboratory selection experiments are used for taxa that have short generation times. Populations are exposed over multiple generations to the stressor of interest and the remaining genotypes can then be compared to controls to see if they have adapted to environmental conditions. *Copepod symbol courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (https://ian.umces.edu/symbols/).*

Paganini, 2015). These short generation species are well equipped for rapid evolutionary responses to ocean change and present unique opportunities to quantify evolutionary responses of populations to ocean change stressors (Peijnenburg and Goetze, 2013).

The ability of the different populations to respond to selection by various stressors are tested by exposing them over multiple generations to the stressor of interest and the remaining genotypes can be compared to controls to see if they have adapted to environmental conditions (Collins et al., 2013; Dam, 2013; Lohbeck et al., 2012). For example, exposure of the coccolithophore *E. huxleyi* to low pH over 500 asexual generations (conditions that were deleterious to the original parental clones) resulted in restoration of growth and calcification in the selected clones (Lohbeck et al., 2012). Genes related to pH regulation and carbon transport were upregulated in the selected *E. huxleyi* populations, a potential molecular mechanism related to adaptation to low pH (Lohbeck et al., 2014).

In contrast, in a laboratory study, the intertidal copepod *Tigriopus californicus*, exhibited little adaptive potential across 10 generations in response to increased temperature (Kelly et al., 2011). For the benthic copepod *T. battagliai*, exposure of several generations to low-pH conditions resulted in a reallocation of energy resources to maintain reproductive output, but at a cost with decrease in somatic growth (Fitzer et al., 2012).

There is now considerable interest in understanding the importance of transgenerational effects in response to ocean change as detailed later.

3.5 Genetic Correlations; Interactions Across Multiple Environments

Genetic correlations are useful for understanding the performance of genotypes in response to different environments and accompany identification of G × E interactions because they clarify the relationship across multiple environments (Sgrò and Blows, 2004). For example, in multistressor studies, genetic correlations can reveal whether adaptation to multiple stressors can occur simultaneously (Fig. 6) (Clark et al., 2013; Foo et al., 2012, 2014; Sgrò and Blows, 2004). A genetic correlation is the proportion of variance that two genetic traits share and is central to understanding evolutionary processes (Astles et al., 2006). A trait expressed in multiple environments is treated as two different traits and so a high genetic correlation indicates that the same set of genes influences the two traits similarly and that genotypes would be consistent across environments. For example, Clark et al. (2013) found positive genetic correlations between 120-h old embryos of the marine alga *Hormosira banksii* grown in control (20°C) and increased (28°C) temperature treatments, indicating that genotypes that performed well in the control also performed well at elevated temperatures. Furthermore, positive genetic correlations for the sea urchin *C. rodgersii* indicated that embryos that performed best in increased temperature scenarios also performed best in a low-pH environment (Foo et al., 2012).

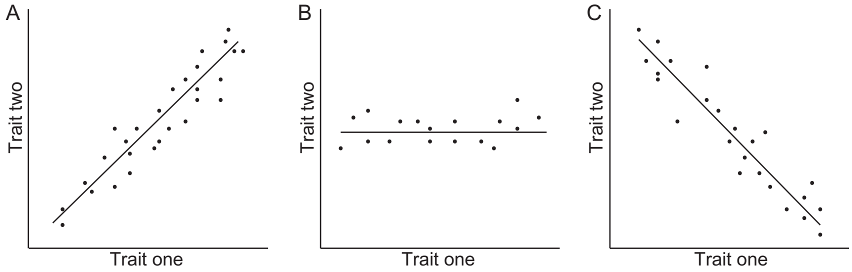

Fig. 6 Examples of possible genetic correlations. Genetic correlations calculate the proportion of variance that two traits share. If similar genes influence both traits, this is evident of a positive genetic correlation (A). If different sets of genes influence both traits, this is evident of a correlation of zero (B). If performance in trait one will have trade-offs with performance in trait two, this is evident of a negative genetic correlation (C).

The genetic correlation across environments becomes lower with more pronounced G × E interactions. If the correlation is zero, the performance of a genotype in one environment does not predict its performance in another. However, negative genetic correlations indicate that the performance in one environment has trade-offs with performance in the other environment, a key prerequisite for evolutionary specialization (Fig. 6) (Eisen and Saxton, 1983). For example, if a negative genetic correlation was found in performance across decreased pH and increased temperature levels, adaptation to simultaneous warming and acidification is unlikely (see Sgrò and Blows, 2004). Although genetic variance may be present, calculating genetic correlations is essential to determine if adaptation to increased temperature and acidification is unconstrained by negative genetic correlations (Blows and Hoffmann, 2005).

3.6 Heritability

Heritability is the proportion of phenotypic variation (V_P) due to variation in genetic values (V_G) and is based on the alleles that are inherited. The effect of alleles depends on their frequency in the population (Falconer and Mackay, 1996). Broad-sense heritability of a trait is defined as the proportion of trait variation that is due to genetic effects, and thus includes all potential sources of genetic variation (additive, maternal, paternal, dominance and epistasis effects) (Hoffmann and Merilä, 1999). An example for marine species has been documented in one study where parents of corals from warm latitudes delivered greater thermotolerance to their offspring compared to parents from cooler latitudes (Dixon et al., 2015). Broad-sense heritability accounted for 87% of larvae survival (Dixon et al., 2015).

Narrow-sense heritability is the proportion of genetic variation due to additive genetic effects only and describes the degree of resemblance between relatives (Hoffmann and Merilä, 1999). In the polychaete *Hydroides elegans*, for example, the narrow-sense heritability of egg size was determined to be 0.45, which may indicate that there is significant potential for egg size to respond to selection pressures such as ocean change (Miles et al., 2007).

There is often no distinction made between broad and narrow-sense heritability. Narrow sense is most commonly used in animal and plant selection programmes because the response to selection depends on only additive genetic variance (Falconer and Mackay, 1996; Hill et al., 2008; Lynch and Walsh, 1998). Heritability is estimated by measuring the extent to which the offspring resemble the parents (Kruuk, 2004; Kruuk et al., 2000).

Because it is not often possible to observe similarity between two generations (parents and offspring), heritability is often measured across one generation (Lynch and Walsh, 1998). The design of the NCII method allows variance to be separated into paternal, maternal, interaction and error effects (Lynch and Walsh, 1998). Heritability is calculated as the ratio between variance components and can be calculated by partitioning total phenotypic variance (V_P), ie, the trait of interest, into genetic (V_G) and environmental variance (V_E) components obtained through Analysis of Variance (ANOVA).

Sunday et al. (2011) calculated narrow-sense heritability for larval sea urchins and mussels in low-pH conditions. By incorporating calculation of heritability into the breeder's equation to simulate the response to selection, they determined that the sea urchin *Strongylocentrotus franciscanus*, was likely to have a faster evolutionary response than the mussel *Mytilus trossulus*. Similarly, heritability was calculated for sea urchins in multistressor environments by Foo et al. (2014), where the dam contribution was much larger at fertilization than at gastrulation, suggesting that performance at the prezygotic stage was dominated by maternal effects and less so for the postzygotic stage. Sire effects were similar in both developmental stages (Foo et al., 2014).

In clonal studies, variation within clones gives an estimate of V_E where variation among colonies is due to $V_G + V_E$. Therefore genetic variation among colonies (V_G) can be estimated by calculating $V_P - V_E$ (Császár et al., 2010). In laboratory selection experiments with fast generation marine species (eg, copepods), similarities between parents and offspring can be observed directly through the change in genotype frequency between generations, but may include nongenetic contributions such as epigenetic effects (Collins et al., 2013).

4. TRANSGENERATIONAL AND MULTIGENERATIONAL EFFECTS FROM EXPOSURE TO ENVIRONMENTAL STRESSORS

Transgenerational effects are the influence of parental environmental history on offspring performance/phenotype. In this case, gene expression patterns are passed from one generation to the next and are not explained by changes to the DNA sequence. Transgenerational effects can result in preadapted offspring that exhibit traits associated with increased fitness in the environmental conditions experienced by their parents (Ross et al., 2016). This can be a type of transgenerational plasticity (Fig. 7), or can be due to differential selection for favourable alleles in a population (Salinas

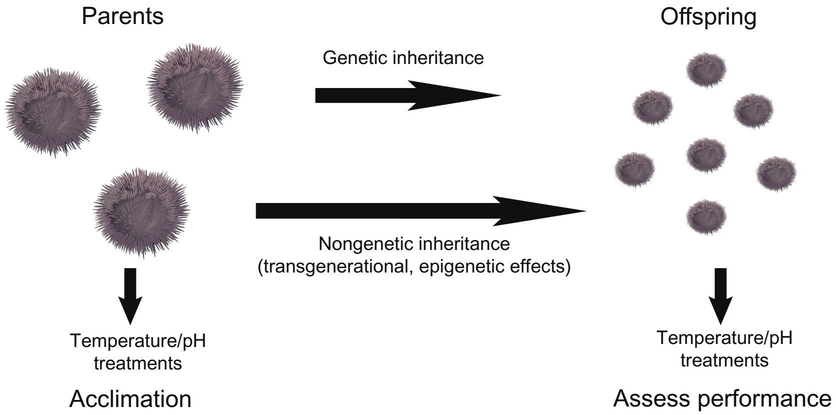

Fig. 7 The performance of offspring in a changing ocean can be influenced by both genetic effects and transgenerational effects when their parents have experienced a similar environment. Acclimation of parents to experimental conditions erases/reduces the influence of physiological history. The parents are conditioned to a new environment during gamete development. Performance of the offspring can then be assessed by considering morphological traits, changes in physiology and the epigenome. *Sea urchin symbol courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (https://ian.umces.edu/symbols/).*

and Munch, 2012). Transgenerational studies involve exposure of parents to experimental conditions during reproductive conditioning (ie, gamete development). The gametes of these parents are used to generate the F1 population. The resultant offspring are then exposed to the environments the parents were exposed to, to determine whether parental exposure influences offspring performance (Salinas et al., 2013). In most transgenerational studies of marine invertebrate species, adults are acclimated in environmental conditions and performance of offspring is assessed to determine whether resilience can be transferred across a generation (see Parker et al., 2015; Ross et al., 2016; Salinas and Munch, 2012). Transgenerational effects are evident in the transition from larvae to juvenile (Hettinger et al., 2012; Pechenik, 1989). Whether these positive effects are able to persist into adulthood and further on into the next generation is less understood (Parker et al., 2015). Multigenerational experiments are much less common as these are complex for long generation species (eg, corals).

4.1 Transgenerational Effects

Research on transgenerational effects has indicated that they can both facilitate and impede genetic evolution (Chevin et al., 2010; Merilä, 2015).

In addition, these effects may also be driven by gender differences and different selection pressures (Lane et al., 2015).

Transgenerational plasticity in response to climate change stressors has been shown in studies of the damselfish *Acanthochromis polyacanthus*, where exposure of parents to environmental conditions (ie, increased temperature and acidification), reduced the negative impacts of the stressors on their offspring (Donelson and Munday, 2015; Munday, 2014; Salinas et al., 2013). Donelson et al. (2011) found that the negative effects of warming were completely ameliorated when previous generations were exposed to the same elevated temperatures. Similar transgenerational plasticity was seen in the minnow *Cyprinodon variegatus* (Salinas and Munch, 2012). For juveniles, parental exposure to low pH increased juvenile survival of anemone fish, *Amphiprion melanopus*, in low-pH conditions, and these individuals had much higher survival rates than juveniles whose parents were sourced from ambient conditions (Miller et al., 2012). Similar results were observed for the Atlantic silverside, *Menidia menidia* (Murray et al., 2014), and for offspring of the three-spined stickleback, *Gasterosteus aculeatus* (Schade et al., 2014). For the oyster, *S. glomerata*, adults exposed to decreased pH for 5 weeks during reproductive conditioning produced larvae with reduced development time and increased body size when raised in similar conditions (Parker et al., 2012).

Transgenerational effects can change with season. For instance, success of Atlantic silverside, *M. menidia*, offspring in reduced pH, corresponded with seasonal pH fluctuations in the parents' habitat (Murray et al., 2014). More recently, the molecular processes underlying transgenerational acclimation to increased temperature were investigated using *A. polyacanthus*. For offspring whose parents were acclimated to increased temperature, there was an upregulation of immune and stress related genes better equipping the juveniles to cope with thermal stress (Veilleux et al., 2015).

Gender also influences transgenerational effects. Performance of tubeworm, *H. elegans*, offspring from parents acclimated in control and low-pH environments in the laboratory, was mediated by parental acclimation (Lane et al., 2015). Different influences were observed between genders, with growth rate for offspring of females acclimated to low-pH conditions decreased in control conditions, a result not found for males (Lane et al., 2015).

Sex determination in *A. polyacanthus* is temperature dependent. Specimens were raised over several generations in multiple ocean warming scenarios to investigate the potential of transgenerational plasticity to ameliorate some impacts of climate change (Donelson and Munday, 2015). For temperatures of +1.5°C above present day average conditions, there was complete restoration of the normal offspring sex ratio of 0.5 (equal numbers of male and female offspring) after one generation. At +3°C, however, there was only a limited improvement in sex ratio even after two generations of rearing at the elevated temperature, and the proportion of female offspring was greatly reduced. These results indicated the potential for transgenerational plasticity to mitigate some effects of ocean warming (Donelson and Munday, 2015).

The timing of parental acclimation may also influence offspring responses. For example, for specimens of the sea urchin *Psammechinus miliaris*, longer adult preexposure to lowered pH reduced larval survival (Suckling et al., 2014). After 17 days, offspring sourced from parents preexposed to low pH for 42, and 70 days were larger than those preexposed for 28 days and ambient sourced offspring directly transferred to low pH (Suckling et al., 2014). For the sea urchin *Strongylocentrotus droebachiensis*, when adults were acclimated for 4 months, fewer offspring compared to the control successfully developed into juveniles when exposed to low pH. However, when adults were acclimated for 16 months, there was no difference in larval survival in response to low pH in comparison with the control (Dupont et al., 2013). Exposure of the sea urchin *Echinometra mathaei* to low pH for 7 weeks did not improve performance of larvae in low pH (Uthicke et al., 2013).

Ideally, acclimation periods for adults should cover the minimal length of time needed for negative effects of ocean stressors to disappear, which varies for different species (eg, Sydney rock oyster, five weeks; Antarctic sea urchin, eight months; Green sea urchin, *S. droebachiensis*, 16 months) (Dupont et al., 2013; Parker et al., 2012; Suckling et al., 2015). The duration and pattern of gametogenesis (eg, time required for egg development, number of oocyte generations) is a key consideration when assessing appropriate acclimation period (Suckling et al., 2014).

Carry over effects do not necessarily translate into increased survival and are not always positive (Parker et al., 2015). Antarctic sea urchin adults exposed to oxidative stress produced eggs with greater levels of antioxidants when compared to control specimens. Despite this inherited potential for resilience, embryo development was similar between acclimated and nonacclimated adults implying that this resilience did not translate into a fitness gain (Lister et al., 2015). Moreover, parental acclimation was not observed to improve behavioural or sensory performance in response to decreased pH in specimens of the damselfish *A. polyacanthus* (Welch et al., 2014). This emphasizes that the type of trait assessed (eg, temperature tolerance, calcification, sensory performance) can determine the inferences made in ocean change experiments with respect to the presence of positive or negative transgenerational effects. It is important to assess a suite of traits to better understand the effects of parental environment on performance and the fitness of offspring (Monaco and Helmuth, 2011; Stillman and Paganini, 2015).

4.2 Multigenerational Effects

Parental exposure to climate change can cause transgenerational changes that allow offspring to better endure stressors, with carry over effects persisting over later life history stages and multiple generations. A multigenerational study of the copepod *Pseudocalanus acuspes* raised for two generations in low-pH treatments found that the negative effects of decreased pH were alleviated with a recovery in metabolism and respiration measurements (Thor and Dupont, 2015). Furthermore, the fecundity of the copepods was significantly decreased in low pH if parents were not previously exposed to low pH (Thor and Dupont, 2015).

Parker et al. (2015) examined whether transgenerational effects continued across generations where larvae of the Sydney rock oyster with a prior exposure to decreased pH were raised to adults and spawned, with the F2 generation also raised in low pH. Prior history of larval exposure to decreased pH carried into adulthood, and resilience of the F2 larvae and juveniles were increased with lower abnormality seen in decreased pH treatments in comparison to those with no prior history of low pH exposure (Parker et al., 2015). A caveat of multigenerational experiments is that only the survivors of previous generations are considered. Parker et al. (2015) noted that there was high mortality (46%) during F1 larvae development, which would have created a selected population of adults most tolerant to low pH which were then used for the F2 generation.

More recently, the polychaete *Ophryotrocha labronica* was raised under control and increased acidification scenarios for six generations. For the first two generations, female fecundity was significantly reduced in the low-pH treatment. However, by the third generation there were no differences in female fecundity across treatments. Thus, transgenerational effects enabled the restoration of reproductive output for this species over multiple generations (Rodríguez-Romero et al., 2015).

4.3 Epigenetics

The outcomes of marine climate change quantitative genetic breeding experiments may also be influenced by the epigenome (Vandegehuchte and Janssen, 2014). Transgenerational effects can include epigenetic effects that are heritable changes in the genome, without alteration to DNA (see Fig. 7) (Burton and Metcalfe, 2014; Turner, 2009). Mechanisms that can produce such changes include DNA methylation and modification of histones that alter how genes are expressed without changing the DNA sequence (Cavalli, 2006; Henikoff et al., 2004). Epigenetic inheritance was suggested as the transgenerational mechanism by which parental exposure improved offspring performance to low pH in both the anemone fish and green sea urchin (Dupont et al., 2013; Miller et al., 2012), although this was not verified through investigation of the epigenome (eg, DNA methylation).

DNA methylation is well documented in mammals, but there are very limited data for invertebrates. Investigation of DNA methylation in the Pacific oyster, *C. gigas*, revealed that methylation is common in that oyster's genome (Gavery and Roberts, 2010), where categories of functional genes displayed significantly different levels of methylation, especially with respect to gene families involved in stress and environmental responses. In another study, Antarctic polychaete, *Spiophanes tcherniai*, embryos were raised for 1 month in either control or increased temperature scenarios (+4°C), and DNA methylation in the epigenome was much higher for groups of those cultured at increased temperature treatments in comparison to the control polychaetes (Marsh and Pasquelone, 2014). More research into the patterns of methylation is needed though to understand its contribution to gene regulation in marine invertebrate species.

It is becoming increasingly evident that environmental history of parents, and even of previous generations (eg, grandparents), can have a major influence on the phenotype of offspring through epigenetic effects (Burton and Metcalfe, 2014; Daxinger and Whitelaw, 2010; Ho and Burggren, 2010; Marsh and Pasquelone, 2014). Epigenetic inheritance can allow phenotypic plasticity to cross generations. Where plastic responses in the parents can alter offspring development, plastic responses across generations may facilitate persistence, especially when the environment is changing too rapidly for genetic adaptation (Lloyd Morgan, 1896; Merilä, 2012). Thus, phenotypic change may not always involve adaptive evolution and might be entirely mediated by nongenetic factors (Bonduriansky and Day, 2009). Considering only genetic variation in adaptive capacity studies may not fully identify the actual potential for population persistence (Sunday et al., 2011; Thor and Dupont, 2015).

5. CONCLUSIONS

While numerous marine climate change studies over the last decade have provided insights into the vulnerability of individuals to a single stressor, warming or acidification, and more recently both in combination and with other stressors, a more holistic approach is necessary for future studies. Recent research has used an integrative approach, incorporating multiple stressors and investigating adaptive potential through application of a range of methods such as quantitative genetics, laboratory selection, as well as investigation of phenotypic plasticity and genetic variation present within populations. These studies are providing insights as to whether evolutionary rescue is possible for marine species, and whether human assisted evolution is an avenue to avoid extinction. Furthermore, transgenerational experiments are becoming more tractable. Factors such as adult acclimation time can affect the experimental outcome and whether the transgenerational effects are neutral, positive or negative, and so it will be useful to establish recommended guidelines for experiments regarding the effects of ocean climate change stressors. To estimate the adaptive potential of marine species to a changing climate, there is a need for long-term, multigenerational experiments that capture developmental plasticity, genetic variation and transgenerational effects. It will be essential to measure multiple traits related to morphology and physiology, lethal and sublethal effects and to quantify corresponding changes in the transcriptome, proteome and metabolome. Ultimately, a combined approach will be most informative for making accurate predictions of how marine communities and ecosystems will be altered by climate change. These research improvements may be useful for facilitating the development of effective management strategies to protect marine resources.

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