FISH and FISHERIES

Climate change and the evolution of reef fishes: past and future

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Abstract

Predicting the impacts of ocean warming and acidification on marine ecosystems requires an evolutionary perspective because, for most marine species, these environmental changes will occur over a number of generations. Acclimation through phenotypic plasticity and adaptation through genetic selection could help populations of some species cope with future warmer and more acidic oceans. Coral reef species are predicted to be some of the most vulnerable to climate change because they live close to their thermal limits. Yet, their evolutionary history may indicate that they possess adaptations that enable them to cope with a high CO_2 environment. Here, we first explore the evolutionary history of reef fishes and how their history has shaped their physiological adaptations to environmental temperatures and pCO_2. We examine current-day thermal and CO_2 environments experienced by coral reef fishes and summarize experimental studies that have tested how they respond to elevated temperatures and pCO_2 levels. We then examine evidence for acclimation and adaptation to projected ocean warming and acidification. Indeed, new studies have demonstrated the potential for transgenerational plasticity and heritable genetic variation that would allow some fishes to maintain performance as the oceans warm and become more acidic. We conclude by outlining management approaches – specifically those that can help preserve genetic variation by maintaining population size – to enhance the potential for genetic adaptation to climate change.

Keywords acclimation, adaptation, global warming, ocean acidification, plasticity

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Introduction

Carbon dioxide (CO_2) concentrations in the atmosphere have risen from approximately 280 ppm before the Industrial Revolution to 400 ppm in 2015 (Dlugokencky and Tans 2015), the highest level in at least 800 thousand years (Luthi *et al.* 2008). If the current anthropogenic emissions trajectory is maintained, atmospheric CO_2 will exceed 900 ppm by the year 2100 (Meinshausen *et al.* 2011), a level not seen for at least 30 million years (Myr) (Hönisch *et al.* 2012). The increase in atmospheric CO_2 is causing the Earth to warm, with average global surface temperatures projected to increase by approximately 4 °C (range: 2.6–4.8 °C) and ocean temperatures by 3 °C (range: 2.1–4.0 °C) by the end of the century (Collins *et al.* 2013). Furthermore, the partial pressure of CO_2 (pCO_2) at the ocean surface is rising at the same rate as in the atmosphere, causing ocean pH to decline (ocean acidification; Doney 2010). Ocean pH has already declined by 0.1 units since the Industrial Revolution and is projected to decrease a further 0.4 units by the year 2100 due to the continued uptake of CO_2 from the atmosphere (Pörtner *et al.* 2014). On this trajectory, it is predicted that by the year 2100, there will be extended periods of time where pCO_2 at the ocean surface exceeds 1000 μatm, and the present-day natural oceanic CO_2 oscillations may be amplified by up to 10 fold (McNeil and Sasse 2016). Ultimately, this rapid warming and acidification of the oceans will have far-reaching impacts on marine organisms and the ecosystems they inhabit (Harley *et al.* 2006; Doney *et al.* 2012; Pörtner *et al.* 2014).

Tropical species are predicted to be especially sensitive to climate change because they live in a relatively stable thermal habitat (Tewksbury *et al.* 2008). In general, tropical species have a narrower thermal tolerance range than temperate species and may already be living close to their upper thermal limits (Deutsch *et al.* 2008; Sunday *et al.* 2011). Some tropical species also appear to have a limited capacity to acclimate to higher temperatures (Stillman 2003). Consequently, tropical species may be vulnerable to a rapid climate change because a small increase in temperature could exceed their thermal optimum, causing a decline in individual performance. While the thermal tolerance of temperate- and cold-water fishes has been studied for decades (Wood and McDonald 1997), similar research on coral reef fishes has a much more recent history (Munday *et al.* 2012b). Nevertheless, new studies indicate that some reef fishes are living close to their thermal limits. Temperatures just 1.5–3.0 °C above current-day summer averages reduce the scope for aerobic performance (Nilsson *et al.* 2009; Rummer *et al.* 2014), growth rate (Munday *et al.* 2008b), swimming performance (Johansen and Jones 2011) and reproduction (Pankhurst and Munday 2011), but result in increased food intake and feeding frequency (Johansen *et al.* 2015) in reef fishes. Some species even reach their critical thermal limits just 3–4 °C above current-day average summer temperatures (Rummer *et al.* 2014), limits that may be further reduced by ocean acidification (Munday *et al.* 2009a). Consequently, there is good reason to expect that climate change will have highly significant effects on coral reef fish populations and communities.

Despite the experimental evidence that small increases in temperature can significantly affect individual performance, many reef fishes have large latitudinal ranges, spanning thermal gradients similar to the temperature increases predicted due to global warming. Furthermore, some populations, for example in the Arabian Gulf, already experience water temperatures greater than the maximum projected to occur on most coral reefs due to climate change (Feary *et al.* 2010; Burt *et al.* 2011). These distribution patterns indicate that reef fishes could have a considerable capacity for acclimation or adaptation to higher temperatures. Indeed, recent studies have revealed an unexpected capacity for developmental and transgenerational thermal plasticity in some coral reef fishes (Donelson *et al.* 2011, 2012). Plasticity has also been observed in response to elevated CO_2

levels. For example, the negative effects of projected future CO_2 levels on metabolic rate, growth and survival of juvenile reef fishes are absent if the parents had previously experienced the same elevated CO_2 levels as their offspring (Miller *et al.* 2012). In addition to developmental and transgenerational plasticity, reef fishes may genetically adapt to rising temperatures and ocean acidification over coming decades. While climate change and ocean acidification are occurring at rates unprecedented in recent geological history, they are still occurring over a time span that encompasses a number of generations for most reef fishes. Selection of tolerant genotypes within existing populations could enable the populations of some coral reef fishes to adapt to warmer, more acidic waters. Therefore, an evolutionary perspective is required when attempting to predict the effects of climate change and ocean acidification on reef fish populations (Munday *et al.* 2013a; Sunday *et al.* 2014).

While the projected increase in ocean temperatures due to climate change is not unique over the evolutionary history of coral reef fishes (Norris *et al.* 2013), the rate of warming due to anthropogenic climate change is at least ten times faster than any climate shift that has occurred in the past 50 Myr (Masson-Delmotte *et al.* 2013), the time period over which coral reef fishes have evolved and diversified (Bellwood and Wainright 2002). There was a 3–4 °C increase in sea surface temperature (SST) when the Earth shifted to an interglacial phase 20 (ka: kiloannum or thousand years ago), which is similar to the maximum warming projected for year 2100 due to climate change (Masson-Delmotte *et al.* 2013). However, this warming occurred over approximately 5000 years, not just a few hundred years, as is occurring with contemporary climate change. Similarly, ocean acidification caused by the uptake of anthropogenic CO_2 from the atmosphere is occurring at a rate unprecedented in the last 50 Myr (Doney 2010). The question is, 'Do reef fish possess sufficient plasticity, or can they adapt fast enough to keep pace with the rapid warming and acidification projected to occur over the next 50–100 years?'

In this study, we investigate the potential for reef fish to adapt to anthropogenic climate change. We first explore the evolutionary history of reef fishes and how this has shaped their physiological adaptations to environmental temperature and pCO_2. Next, we examine the current-day thermal and CO_2 environments experienced by reef fishes and summarize recent experimental studies testing how they respond to elevated temperature and CO_2. We then examine evidence for acclimation and adaptation to projected ocean warming and acidification and the methods that can be used to test evolutionary potential. Finally, we consider conservation and management options that could enhance the potential of reef fish populations to cope with a rapidly changing climate. Coral reef habitats are particularly susceptible to ocean warming and acidification (Hoegh-Guldberg and Bruno 2010), and habitat degradation due to these stressors will have substantial effects on reef fishes (Pratchett *et al.* 2008, 2015). We do not specifically examine the evolutionary implications of habitat loss for coral reef fishes, because this topic has received little theoretical or experimental attention to date. Nevertheless, we do consider how habitat degradation will interact with evolutionary potential when considering management strategies for the future.

Evolutionary history and adaptations

The geological timescale over which the fishes have evolved was characterized by four of the Earth's five major mass extinction events, and the dramatic changes in atmospheric oxygen, CO_2 and global temperatures that occurred during these events may have played a profound role in shaping the evolution and diversification of the fishes (Ward 2006). The Silurian and Devonian 'Age of the Fishes', around 400 million years ago (Ma: Mega-annum or million years ago), coincided with a global cooling event, but a prolonged period of elevated atmospheric CO_2 (exceeding 4000 ppm) and low O_2 levels (<15%) (Royer et al. 2004; Clack 2007; Fig. 1a). During this time, the ray-finned fishes – to which modern teleost fishes belong – diverged from the lobe-finned fishes. For the following 150 Myr, the fishes were successful during a time when atmospheric CO_2 levels were falling (from over 4000 ppm to below 500 ppm) and O_2 levels were rising (nearing 30%, compared to today's 21%). The Permian mass extinction, approximately 252 Ma, however, marked a turning point in the evolution of the fishes. For the most part, the lobe-finned fishes were eliminated from the water with modern lineages moving to land, leaving ray-finned fishes to expand and exploit the newly available habitats (Clack 2007). Although the Permian mass extinction resulted in

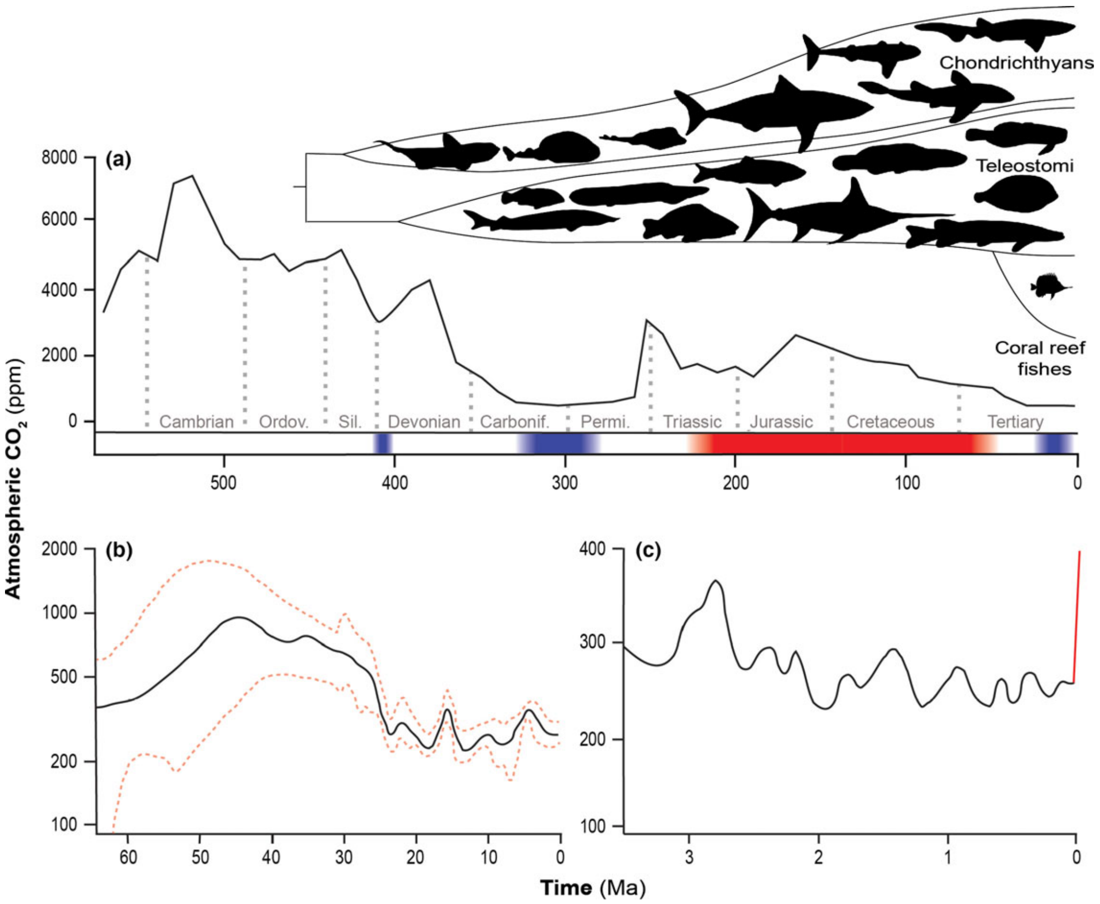

Figure 1 Evolutionary timeline of the Chondrichthyans and Teleostomi, including coral reef fishes, with corresponding atmospheric CO_2 concentrations in parts per million (ppm, *y*-axis) and global warming and cooling periods noted by red and blue shaded bar (a) (Royer et al. 2004; Clack, 2007; Erwin et al. 2011; Kardong, 2012; Cowman and Bellwood, 2013). Panels (b) and (c) show a higher-resolution trajectory of atmospheric CO_2 concentrations over the evolutionary history of the coral reef fishes (redrawn from Masson-Delmotte *et al.* 2013). Dotted lines in (b) indicate 1-standard deviation uncertainty. Red line in (c) indicates a modern increase in atmospheric CO_2 driven by anthropogenic emissions.

a loss of 96% of all marine fish species, this transition also marks one of the most profound radiation events among the teleosts (Randall *et al.* 2014). This radiation occurred despite the fact that volcanic activity was causing atmospheric CO_2 levels to rise again, while O_2 levels were falling and global temperatures were rising (Fig. 1a). It is thought that the teleosts' success during this time of elevated CO_2, low O_2 and warmer temperatures is in part due to their enhanced capacity for O_2 delivery, especially during conditions that would normally preclude efficient O_2 uptake (Rummer *et al.* 2013a; Randall *et al.* 2014). Enhanced O_2 transport opened the path for future radiations due to the modifications in swimming and feeding (Ilves and Randall, 2007; Near *et al.* 2012), all of which contribute to the teleosts being one of the most successful adaptive radiation events in vertebrate history.

The reef fishes, which are a distinct assemblage of fishes in terms of morphology and familial composition (e.g. Acanthuridae, Apogonidae, Chaetodontidae, Labridae, Pomacentridae, Siganidae), represent some of the most diverse groups of vertebrates on the planet. Most reef fishes belong to the order Perciformes and first appear in the fossil record (e.g. Monte Bolca in northern Italy) approximately 65–50 Ma (Choat and Bellwood 1991; Bellwood and Wainright 2002; Goatley *et al.* 2010). Following the Cretaceous–Tertiary mass extinction (K/T boundary, 66 Ma), the major coral reef fish lineages began to emerge, beginning with the Apogonidae (63 Ma) and then Labridae (60 Ma; Cowman and Bellwood 2011). This also marks the time during which the scleractinian corals – the coral taxa that largely dominate modern reefs (e.g. *Acropora*, *Porites* and *Pocillopora*) – first appear in the fossil record (see Choat and Bellwood 1991). The diversification of reef fish families extends into the Early Eocene Optimum (52–48 Ma), which marks the end of a long global warming event, when tropical SST was as much as 5 °C warmer than current-day temperatures and atmospheric CO_2 levels exceeded 1000 ppm (Masson-Delmotte *et al.* 2013; Norris *et al.* 2013; Fig 1a). Therefore, the emergence of the reef fish lineages occurs during a period of much warmer temperatures and higher atmospheric CO_2 levels than the present day (>500 ppm).

While the origin of reef fishes is in the early Tertiary, most reef fish diversified more recently, with the most speciose genera diverging and radiating within the last 23 Myr (Bellwood, 1996; Cowman and Bellwood 2011, 2013; Pellissier *et al.* 2014). This period is characterized by atmospheric CO_2 levels and global temperatures that are more similar to pre-industrial times (Fig. 1b). In fact, 19% of wrasses, 31% of damselfishes, 65% of butterflyfishes and 80% of parrotfishes are estimated to have arisen within the last 3 Myr (Choat *et al.* 2012; Pellissier *et al.* 2014). Consequently, many of the fishes present on today's reefs originated in the Pleistocene, 2.588–0.0117 Ma. While the Pleistocene was characterized by repeated periods of glaciation and dramatic changes in sea level, atmospheric CO_2 was always below 500 ppm and tropical SST was no more than 2 °C above pre-industrial (Masson-Delmotte *et al.* 2013; Fig. 1c). Consequently, much of the diversity of coral reef fishes was generated during a period of relatively low atmospheric CO_2 levels, oxygen levels similar to today (~21%) and tropical SST undergoing a cooling trend if not broadly comparable with the current day. Despite the long evolutionary history of marine fishes, the physiological tolerance of extant coral reef fishes to climate change will have been shaped by their recent evolutionary history and the water quality of the oceans during that time.

Current-day environments and effects of climate change

Temperature

Coral reefs and their associated fish assemblages extend from the equator to subtropical latitudes around 30°; although, a few isolated reefs exist at higher latitudes. Average summer temperatures over this latitudinal gradient differ only by about 5–6 °C, from 30 °C near the equator to 25 °C in the higher latitudes. The latitudinal temperature range is much greater in winter, however with temperatures still around 30 °C near the equator, but falling below 20 °C at high-latitude locations. Consequently, high-latitude reef fish populations typically experience a far greater seasonal thermal range than low-latitude populations. Average SST may vary seasonally by just 1–2 °C near the equator, but by over 10 °C in higher latitudes (Fig. 2). Some of the most extreme temperature ranges experienced by coral reef fishes occur in the southern Persian Gulf, where ocean temperatures can drop to 12 °C in winter months, but exceed 35 °C in the summer (Burt *et al.* 2011). While these reef fish assemblages have lower species richness, abundance and biomass when compared to less extreme habitats in the nearby Gulf of Oman (22–31 °C), they nevertheless indicate that some reef fishes can tolerate an extraordinary range of

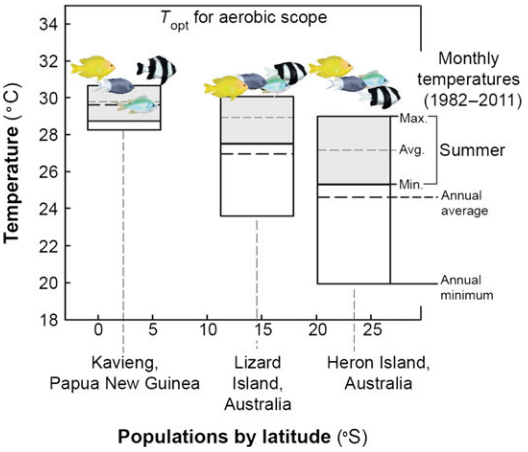

Figure 2 Local temperatures and the temperatures for optimal aerobic performance (T_{opt}) for five species of damselfishes represented by three populations spanning 2321 km from the southern Great Barrier Reef to northern Papua New Guinea. Sampling sites are represented by latitudinal position (°S). *Pomacentrus moluccensis*, *Acanthochromis polyacanthus* and *Chromis atripectoralis* (left to right) are distributed across all three sites, but for the two sister species, *Dascyllus melanurus* and *D. aruanus*, the former was only found in near-equatorial locations. Monthly sea surface temperatures (grey and white rectangles) are from 30 years of Integrated Global Ocean Services System (IGOSS) satellite data. Adapted from Rummer *et al.* 2014.

temperatures and even persist at maximum temperatures greater than the warming projected for coral reefs in most other parts of the world.

Rising ocean temperatures may not be immediately lethal for coral reef fishes (Mora and Ospina 2001), but the decline in performance that can occur before fish reach their lethal temperatures could influence life-history traits and population abundance, or even result in biogeographical redistribution of some species (Munday *et al.* 2008a; Nilsson *et al.* 2009; Rummer *et al.* 2014). Reductions in performance due to warmer temperatures are thought to be related to how temperature influences O_2 uptake, transport and delivery in aquatic organisms, also known as the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis (Pörtner, 2001; Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Eliason *et al.* 2011) . An animal's performance is supported by their scope for aerobic metabolism (aerobic scope), calculated as the difference in O_2 consumption between resting and maximal performance (Fry and Hart 1948; Priede 1977; Pörtner and Farrell, 2008), and represents the oxygen available – beyond that required for basic maintenance – for activities, such as foraging, predator avoidance, migration and reproduction. In principle, aerobic scope generally follows a skewed, bell-shaped curve with temperature. A species will have the greatest aerobic scope at a particular temperature (T_{opt}), beyond which aerobic scope declines due to reduced oxygen supply to the tissues. This pattern has been demonstrated for a number of coral reef fish species. For example, aerobic scope is reduced by as much as 72% in reef fishes acclimated to temperatures just 1–3 °C above their T_{opt} (Nilsson *et al.* 2009; Gardiner *et al.* 2010; Johansen and Jones 2011; Rummer *et al.* 2014). Temperature-induced reductions in aerobic scope have ecological consequences because less energy may be available for vital life-history processes. Indeed, a 2–3 °C increase in average temperature compromises the growth and reproduction of some coral reef fish species (Munday *et al.* 2008b; Donelson *et al.* 2010). Swimming performance is reduced by nearly 28% in five species of coral reef fishes upon acclimation to 32 °C, which is only 3 °C above their summer average temperatures (Johansen and Jones 2011). Likewise, coral trout (*Plectropomus leopardus* Serranidae) exhibit nearly a 50% decrease in spontaneous swimming speeds, a reduction in overall swimming activity, but an increase in food consumption and feeding frequency upon acclimation to temperatures just 3 °C above their summer average temperatures (Johansen *et al.* 2014, 2015). These studies indicate that even small increases in SST could have implications for reef fish populations.

Comparing aerobic scope or other aspects of physiological performance among geographically distinct populations of reef fishes provides a unique opportunity to test whether species exhibit local adaptation to their thermal environment. Interestingly, when the T_{opt} for aerobic scope was compared between three latitudinally distinct populations of damselfishes, ranging from low latitudes near the equator to higher latitudes of the southern Great Barrier Reef, all three populations exhibited a similar temperature at which aerobic scope was the greatest, despite 21° of latitudinal separation (Rummer *et al.* 2014). The T_{opt} was between the summer average and maximum temperatures for populations living near the equator, but for populations living at higher latitudes, T_{opt} exceeded the summer maximum temperatures for those locations (Fig. 2). Consequently, it appears that low-latitude populations of coral reef fishes are already living close to their T_{opt} for aerobic performance and, if adaptation cannot keep pace with increasing temperatures, they may be most vulnerable to a changing climate. In contrast, higher-latitude populations appear to have greater plasticity to cope with elevated temperatures because T_{opt} is above current-day summer temperatures. Consistent with these findings, Iftikar *et al.* (2014) found that tropical wrasses inhabiting narrow thermal ranges exhibited mitochondrial and cardiac failure with elevated temperatures much sooner than their higher-latitude confamilial counterparts. Due to less thermal variability and thus, narrower thermal safety margins, the impact of rising SST on coral reef fishes could be the greatest at low latitudes. If the rate of increasing SST exceeds the rate of adaptation, the consequences could be population declines and potentially the redistribution of equatorial species to higher latitudes (Nilsson *et al.* 2009; Nguyen *et al.* 2011; Sunday *et al.* 2012).

CO_2 and ocean acidification

The average pCO_2 of the ocean is rising at the same rate as the atmosphere from anthropogenic CO_2 emissions (Doney 2010). The oceans absorb about 30% of anthropogenic CO_2 emissions, slowing the rate of CO_2 accumulation in the atmosphere, but causing seawater pH to decline (Doney 2010). Over time scales of days and weeks, the pCO_2 and pH of the open ocean are relatively stable, but can be highly variable in coastal habitats (Hofmann *et al.* 2011). On coral reefs, pH and pCO_2 fluctuate daily and seasonally and are also influenced by reef location and water flow. In shallow reef habitats, there can be significant reductions in CO_2 during the day due to photosynthesis and elevation of CO_2 at night due to respiration, with the CO_2 range strongly influenced by the degree of flushing and exchange with oceanic water by tides and currents. For example, on a mid-shelf reef flat in the Great Barrier Reef, pCO_2 ranged from 325–542 μatm in summer and 275–420 μatm in winter (Albright *et al.* 2013). Average CO_2 levels are typically elevated near coral reefs in summer due to higher rates of respiration and calcification that release CO_2. On a shallow reef flat within an enclosed coral reef lagoon, pCO_2 varied from 150–1325 μatm in summer and 70–892 μatm in winter (Shaw *et al.* 2012). Therefore, for brief periods each day, reef fish in some habitats already experience pCO_2 levels similar to those projected for the open ocean by the end of this century (Shaw *et al.* 2013).

Given their evolutionary history (Fig. 1), CO_2 tolerance in marine fishes may be expected, and accordingly, most physiological studies to date have been purely mechanistic, that is examining the mechanisms related to maintaining oxygen transport and acid–base/ion regulation in a high CO_2 environment (Brauner and Baker 2009; Rummer *et al.* 2013a; Heuer and Grosell 2014; Randall *et al.* 2014). A general trend is that the effects of elevated CO_2 on overall physiological performance – if any – initially originate from the acid–base disturbance and added energy required for pH compensation. In most fishes, pH compensation is limited by the intrinsic capacity for bicarbonate ($[HCO_3^-]$) accumulation via counter ions (e.g. [Cl−], $[Na^+]$) and/or H^+ extrusion, which for marine species largely occurs at the gill (Baker *et al.* 2009; Brauner and Baker 2009; Heuer and Grosell, 2014). Most marine fishes studied to date are readily able to use these mechanisms to defend against plasma acidosis that results from elevated environmental CO_2, but over extended periods of time this could incur additional energetic costs (Ishimatsu *et al.* 2008). Furthermore, the capacity to compensate for an acid–base disturbance acutely may not necessarily confer tolerance or translate to fitness over the long term.

While based on just a few studies thus far, the physiological effects of elevated CO_2 levels on coral reef fishes have been mixed. For example, metabolic rate and aerobic performance of some species appear to be negatively affected by near-future CO_2 levels (Munday *et al.* 2009a; Miller *et al.* 2012), whereas other species exhibit either no change (Couturier *et al.* 2013; Heinrich *et al.* 2014; Munday *et al.* 2014) or even enhanced scope for aerobic performance (Couturier *et al.* 2013; Rummer *et al.* 2013b). Similarly, juvenile growth was reduced by near-future CO_2 levels in one species of damselfish (Miller *et al.* 2012), unaffected in another (Munday *et al.* 2011) and enhanced in yet another closely related species (Munday *et al.* 2009b). The reasons for this variation are unknown, but could be related in part to the differences in lifestyle and habitat use, which could influence CO_2 tolerance. For example, although not a coral reef fish, as defined in this review, the reef-associated epaulette shark (*Hemiscyllium ocellatum* Hemiscylliidae) is unaffected by exposure to near-future CO_2 levels (Heinrich *et al.* 2014), possibly because it is adapted to sheltering in shallow reef habitat where it already encounters pCO_2 far greater than that predicted for the open ocean by the end of the century. Moreover, no differences could be detected in growth or survival in epaulette shark embryos reared *in ovo* under current-day conditions versus ocean acidification conditions predicted for the year 2100 (Johnson *et al.* 2016). By and large, conclusions about the physiological sensitivity of reef fishes to elevated CO_2 are based on whole-organism responses that may not be sensitive enough to pick up the fine-scale adjustments made at the tissue and cellular levels. Longer-term studies in more realistic and challenging environments (e.g. conditions simulating the natural fluctuations within a coral reef with appropriate adjustments for climate change scenarios) may be required to properly assess the physiological effects of elevated CO_2 on individual performance.

One area where elevated CO_2 has been found to have obvious and consistent effects is on the behaviour of coral reef fishes. When continuously exposed to near-future CO_2 levels for more than a few days, there are changes in olfactory (Munday *et al.* 2009c), auditory (Simpson *et al.* 2011) and visual function (Chung *et al.* 2014). Activity levels (Munday *et al.* 2010), response to chemical cues (Dixson *et al.* 2010; Ferrari *et al.* 2011a), startle behaviour (Allan *et al.* 2013) and learning ability (Ferrari *et al.* 2012) are all affected in larval and juvenile reef fishes. These changes in behaviour alter the outcome of predator-prey (Ferrari *et al.* 2011b; Allan *et al.* 2013) and competitive (McCormick *et al.* 2013) interactions. The effects are not restricted to larvae and small juveniles. For example, exposure to elevated CO_2 reduced homing success in adult cardinalfishes (Devine *et al.* 2012) and altered the attraction of a meso-predator, *Pseudochromis fuscus* (Pseudochromidae), to the olfactory stimulus of injured prey (Cripps *et al.* 2011). Clearly, these broad-ranging effects on behaviour could have implications for population dynamics and the structure of reef fish communities.

The behavioural changes observed in coral reef fishes exposed to elevated CO_2 appear to be caused by acid–base regulation interfering with the function of GABA-A receptors, the primary inhibitory neurotransmitter receptor in the vertebrate brain (Nilsson *et al.* 2012; Hamilton *et al.* 2014). Under normal conditions, ion gradients over the neuronal membrane result in an inflow of Cl^- and HCO_3^- upon binding of the GABA-A receptor, which then leads to hyperpolarization and inhibition of the neuron. However, when fish are exposed to elevated environmental CO_2, pH compensation will change ion concentrations that could alter the receptor function. Depending on the magnitude of changes in Cl^- and HCO_3^- during acid–base regulation, resultant alterations in ion gradients could either potentiate GABA-A receptor function or reverse its action, making it excitatory rather than inhibitory (Heuer and Grosell 2014).

The effects on fish behaviour and sensory abilities occur when fish are exposed to more than 600 μatm CO_2 for more than 2–3 days (Munday *et al.* 2010, 2012a), well within the projected range of CO_2 levels projected to occur by the end of this century (Meinshausen *et al.* 2011). Interestingly, few behavioural effects have been detected below 600 μatm and none below 500 μatm CO_2, which are at the upper range of pCO_2 that reef fish likely experience for a few hours at night on most coral reefs in summer (e.g. Albright *et al.* 2013). This suggests that behaviour is adapted to the daily CO_2 fluctuations on coral reefs, but is sensitive to continuous exposure to elevated CO_2 levels that are outside this range (e.g. >600 μatm). Studies that link the timing of behavioural and acid–base regulatory responses to CO_2 fluctuations in coral reef environments are now needed to determine thresholds beyond which rising oceanic pCO_2 will interact with daily pCO_2 fluctuations to affect the behaviour of fishes living in shallow reef habitats (Shaw *et al.* 2013).

Interactions between temperature and CO_2

As described above, the effects of projected future temperature increases (1.5–3 °C) on the physiology and life-history traits of reef fishes appear to be far greater than the likely effects of elevated CO_2 levels that will drive these thermal changes. One recent study supports this observation, with the effects of elevated CO_2 (i.e. moderate, 644 μatm and high, 1134 μatm) on reproduction in the cinnamon anemonefish being dwarfed by the effects of temperature (Miller *et al.* 2015). However, these stressors can also interact in important ways. For example, elevated temperatures could add to the metabolic costs associated with exposure to elevated CO_2, and at least one study on coral reef fishes so far suggests that the combined effects of temperature and CO_2 on aerobic scope could be more pronounced than either factor alone (Munday *et al.* 2009a). Furthermore, elevated temperature can intensify or mask the effects of elevated CO_2 on fish behaviour. In a predator-prey experiment, Ferrari *et al.* (2015) found the elevated temperature and CO_2 interacted synergistically on overall predation rate, but antagonistically on predator selectivity. Predation rate more than doubled when predators and prey were exposed to both stressors compared with either in isolation. These new studies demonstrate that it will be critical to consider the interacting effects of elevated temperature and CO_2 when testing the capacity to adapt to future change. Testing responses to either factor in isolation may be insufficient to assess the direction or magnitude of evolutionary responses, especially if there are genetic correlations or trade-offs that could constrain adaptation when both temperature and pCO_2 are changing together (Munday *et al.* 2013a; Sunday *et al.* 2014).

Plasticity and evolutionary potential

While there is increasing experimental evidence that temperatures and pCO_2 levels projected for the tropical oceans in the second half of this century have significant effects on the physiology and ecology of coral reef fishes, there is also evidence that at least some species or populations have some capacity to adapt to these changes. As described above, many reef fishes have geographical ranges spanning latitudinal temperature gradients at least as great as the projected temperature increases due to climate change (Munday *et al.* 2008a; Rummer *et al.* 2014). These species must either exhibit a substantial plasticity in thermal tolerance throughout their geographical range, or populations must be adapted to the local thermal environment. While there are not similar geographical gradients in pCO_2, diverse reef fish communities persist in localized areas of elevated CO_2, such as volcanic seeps (Munday *et al.* 2014) and upwelling regions in the Eastern Pacific (Manzello 2010). These sites are not perfect analogues for ocean acidification, but the persistence of fish communities at these sites indicates that some species can tolerate CO_2 levels similar to those predicted more generally for the ocean by 2100.

Phenotypic plasticity

Acclimation through phenotypic plasticity may allow marine organisms to persist in the face of environmental change and provide time for populations to genetically adapt over the longer term (Munday *et al.* 2013a). For long-lived species, such as some coral reef fishes, phenotypic plasticity is likely to be especially important in responding to climate change because their generation time is relatively slow compared with the rate of climate change (Crozier and Hutchings 2014). Three general forms of plasticity are recognized (Angilletta 2009): (i) reversible plasticity that occurs over days to months, for example, in response to the seasonal variation, (ii) developmental plasticity, where exposure to an environmental condition early in life influences performance in that environment later in life, and (iii) transgenerational plasticity, where the environmental conditions experienced by parents have a significant effect on the performance of the offspring in that environment (Fig. 3). Animals can improve their performance in a new environment (i.e. acclimate) through one or more of these forms of phenotypic plasticity. Acclimation through developmental and transgenerational plasticity is especially important in a climate change context, because animals in the future will experience elevated temperature and pCO_2 throughout their lifespan and across generations.

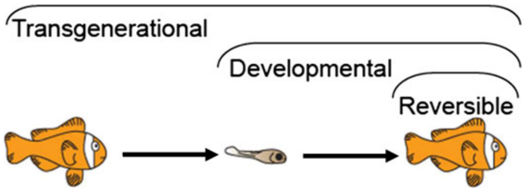

Figure 3 Three general forms of phenotypic plasticity that can enable the animals to acclimate to new environmental conditions: (i) reversible plasticity that occurs over days to months, for example, in response to seasonal variation, (ii) developmental plasticity, where exposure to an environmental condition early in life influences performance in that environment later in life, and (iii) transgenerational plasticity, where the environmental conditions experienced by parents have a significant effect on the performance of the offspring in that environment.

Thermal acclimation

Tropical species are predicted to exhibit less potential for thermal acclimation than higher-latitude species because they live in a more thermally stable environment and have limited need to adjust to seasonal temperature variation (Stillman 2003; Tewksbury *et al.* 2008). Furthermore, many may already be living close to their upper thermal limits (Deutsch *et al.* 2008; Sunday *et al.* 2011; Rummer *et al.* 2014). Consistent with this prediction, most coral reef fishes tested to date appear to have a limited capacity for short-term thermal acclimation. For example, a 3 °C increase in water temperature caused increased oxygen consumption and reduced hypoxia tolerance in the cardinalfish, *Ostorhinchus doederleini* (Apogonidae), and damselfish *Pomacentrus moluccensis* (Pomacentridae), and there was no improvement after 7 or 22 days of exposure to the higher temperature (Nilsson *et al.* 2010). Elevated temperatures (1.5–3 °C) reduce aerobic scope and reproductive output of *Acanthochromis polyacanthus* (Pomacentridae) even after 12 months or more exposure in a seasonally fluctuating environment (Donelson *et al.* 2010; G. Rodgers unpublished data). The reduction in aerobic scope of *A. polyacanthus* is the same in fish exposed to higher temperatures for just a few days or 12 months, demonstrating no potential for reversible thermal acclimation in adults.

In contrast to the limited capacity for thermal acclimation in adults, some coral reef fishes are able to developmentally acclimate to higher temperatures. Donelson *et al.* (2011, 2012) found that *A. polyacanthus* 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 moved to the warmer temperature later in life. In other words, development at +3 °C during early life improved performance at +3 °C later in life. However, developmental acclimation did not fully restore the metabolic rate to levels observed in current-day conditions, indicating limitations to increased performance through this process. Furthermore, there was no improvement in metabolic rate at +1.5 °C, suggesting that the energetic cost of developmental acclimation may have outweighed the benefits at this more moderate temperature.

Developmental thermal acclimation has also been observed in reproductive performance, but with contrasting patterns to metabolic rate (Donelson *et al.* 2014). At +1.5 °C above present-day temperatures, reproductive output of *A. polyacanthus* was improved to match fish maintained at present-day temperatures when fish complete their development at the higher temperature. However, reproductive acclimation was not observed in fish reared at +3 °C, suggesting limitations to what is possible within one generation. Furthermore, the improvements seen in reproduction did not match the pattern of thermal acclimation in metabolic rate. Fish reared at +1.5 °C, with the greatest capacity for reproductive acclimation, exhibited no acclimation of metabolic rate. Conversely, pairs reared at +3 °C, exhibiting acclimation in metabolic rate, demonstrated little capacity for reproductive acclimation (Donelson *et al.* 2014). This indicates that there may be different capacities for developmental thermal acclimation among physiological and life-history traits and that multiple traits need to be considered to determine how developmental acclimation could assist coral reef fishes in coping with climate change.

An unexpected discovery was the complete compensation of aerobic scope at high temperatures through transgenerational plasticity (Donelson *et al.* 2012). Aerobic scope of *A. polyacanthus* declines sharply at 1.5 and 3.0 °C above the current-day summer average temperature, but is restored to control levels when both offspring and their parents experience the same elevated temperature (Fig. 4). Similar transgenerational thermal acclimation occurs in the sheepshead minnow, *Cyprinodon variegatus* (Cyprinodontidae), where juveniles grow faster at higher temperatures if their parents have been exposed to the high temperature (Salinas and Munch 2012). Furthermore, biased sex ratios in *A. polyacanthus* caused by development at elevated temperatures do not occur when parents have also developed and matured at elevated temperatures (Donelson and Munday 2015). These studies indicate that transgenerational plasticity could be an important process in adaptive responses of reef fishes to climate change, with performance potentially restored over several generations. While the mechanisms of transgenerational acclimation are currently unknown, these studies show that this could be an important process by which coral reef fishes, and probably other marine organisms, could cope with projected future climate change (reviewed by Salinas *et al.* 2013; Munday 2014) and could enable populations to persist in the face of climate change until

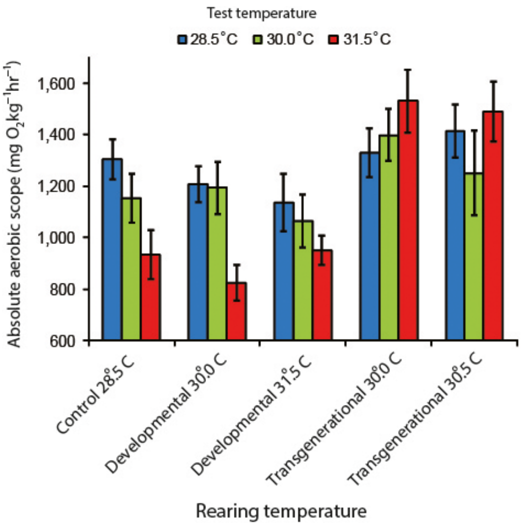

Figure 4 Transgenerational acclimation of aerobic scope in *Acanthochromis polyacanthus*. Aerobic scope is lower in juvenile damselfish at elevated temperatures (30.0 °C and 31.5 °C) compared with controls (28.5 °C) when parents did not experience the elevated temperatures (no-acclimation and developmental acclimation groups). However, aerobic scope in juveniles at elevated temperatures is restored to control levels when parents have been reared their entire life at elevated temperatures (transgenerational acclimation groups). Figure from Donelson *et al.* 2012.

genetic adaptation catches up (Chevin *et al.* 2010).

CO_2 acclimation

Similar to the effects of temperature, there is no evidence for reversible acclimation to elevated environmental CO_2 in reef fishes, especially in relation to the effects on behaviour. For example, behavioural impairment in juvenile coral trout is identical in fish exposed to elevated CO_2 for one month compared with 4 days (Munday *et al.* 2013b). In contrast to thermal effects, however, there is currently no evidence for developmental acclimation to elevated CO_2. Juvenile clownfish reared from hatching under elevated CO_2 conditions exhibit behavioural problems identical to juveniles exposed to elevated CO_2 for 3–4 days (Munday *et al.* 2010). Furthermore, reef fish at natural CO_2 seeps exhibit behavioural effects similar to fish exposed to elevated CO_2 in laboratory experiments, despite having lived in an elevated CO_2 environment since settlement (Munday *et al.* 2014). These studies demonstrate that exposure to elevated CO_2 during early life does not improve behavioural responses in elevated CO_2 later in life. Furthermore, there may be the limited capacity for transgenerational acclimation of behaviour under elevated CO_2 conditions. Welch *et al.* (2014) found that impaired behaviour in juvenile *A. polyacanthus* at 656 μatm and 912 μatm was not improved or reversed in offspring whose parents had also been reared at the same elevated pCO_2 conditions. The lack of behavioural acclimation to elevated CO_2 is important as it indicates that genetic adaptation will be necessary to overcome behavioural problems in a future high CO_2 ocean.

While there is a limited evidence for transgenerational acclimation of behavioural effects to elevated CO_2, physiological and life-history traits are restored when both parents and offspring experience the same elevated CO_2 environment. Miller *et al.* (2012) found that negative effects of elevated CO_2 on metabolic rate, growth and survival of the anemonefish, *Amphiprion melanopus* (Pomacentridae), were absent in juveniles when parents are also exposed to elevated CO_2. A similar phenomenon was recently described in natural populations of Atlantic silverside (*Menidia menidia* Atherinopsidae). Juveniles spawned early in the season, when parents experienced relatively high seawater pH, were highly sensitive to acidified seawater. Later in the season, however, when parents experienced much lower seawater pH while spawning, the survival of juveniles reared in acidified water was similar to controls (Murray *et al.* 2014). Why transgenerational acclimation to elevated CO_2 should occur in some metabolic and life-history traits, but not in behavioural traits, is currently unknown, but is important to understand if we are to accurately predict the effects of climate change and ocean acidification on reef fish populations.

Adaptation

To date, no studies have specifically tested for heritable genetic variation of climate-sensitive traits in coral reef fishes, and only a handful of studies have explored this issue in marine fishes, all of which have involved temperate-water fishes (e.g. Kovach *et al.* 2012; Schade *et al.* 2014; Munoz *et al.* 2015). In one of the most complete studies to date, Munoz *et al.* (2015) used a quantitative genetics breeding design to test for both plasticity and heritable genetic variation in cardiac function in chinook salmon (*Oncorhynchus tshawytscha* Salmonidae). They found a significant plasticity and additive genetic variation in the temperatures for optimum and maximum heart rate. This means that there is a significant potential for evolutionary adaptation of these important traits as river temperatures rise. However, the arrhythmic temperature of the heart exhibited little plasticity or heritable genetic variation. Consequently, salmon populations may be able to adapt to moderate warming, but would become highly vulnerable if river temperatures in future were to exceed the arrhythmic temperature of the heart (24.5 °C in the studied population). On the other hand, the breeding design revealed a significant variation in the arrhythmic temperature of juveniles that could be attributed to mothers (Munoz *et al.* 2015). This suggests that the way mothers resource their eggs can influence the cardiac function of their offspring. For example, larger eggs may produce fitter offspring with stronger hearts. This provides some hope that plasticity and heritability of maternal provisioning could potentially help juvenile salmon adapt to higher river temperatures in future.

The absence of similar studies with coral reef fishes is perhaps surprising given the well-developed techniques for estimating evolutionary potential and the suitability of broadcast-spawning marine species to quantitative genetics approaches (Munday *et al.* 2013a). However, a limitation for using quantitative genetics breeding designs, where a number of males are cross-bred with a number of females to examine the phenotypic variation of the offspring within and among family lines, is that the life cycle cannot be reliably closed in most broadcast-spawning reef fishes. While it may be possible to cross-breed males and females, the techniques to rear the larvae of most broadcast-spawning reef fishes have not been perfected. As a result, it is not yet possible to compare the phenotypic traits of full- and half-siblings from controlled breeding designs with these species. While some demersal-spawning reef fishes, such as some damselfishes and anemonefishes, can be readily reared in captivity, their mode of spawning and the presence of paternal egg care make it complicated to cross-breed a number of different males and females. Cross-fostering is an alternative approach that can be used to test the evolutionary potential in these fishes (Johnson *et al.* 2010), which could be a useful method for testing heritable genetic variation in climate-sensitive traits in demersal-spawning reef fishes for which laboratory culturing is possible.

Heritable genetic variation has also been detected in the sensitivity of fishes to ocean acidification. Malvezzi *et al.* (2015) found that survival of juvenile Atlantic silverside under elevated CO_2 had a significant additive genetic component that might favour adaptation to ocean acidification. In coral reef fishes, Munday *et al.* (2012a) demonstrated that there was selective mortality of juvenile reef fishes associated with their behavioural sensitivity to elevated CO_2. Individuals whose behaviour was most strongly affected by 700 μatm CO_2 suffered higher mortality from predation compared with individuals whose behaviour was unaffected by this moderate increase in pCO_2 (Fig. 5). This is an important first step, as it demonstrates a strong selection for CO_2-tolerant phenotypes, but whether individual variation in CO_2 sensitivity is heritable is currently unknown. Another unresolved issue is whether the selection for thermal tolerance and CO_2 tolerance will act in the same direction on genetic variation. Adaptation will be favoured if the direction of selection is positively correlated, but could be constrained if the selection for thermal and CO_2 tolerance acts in different directions on standing genetic variation (Munday *et al.* 2013a; Sunday *et al.* 2014).

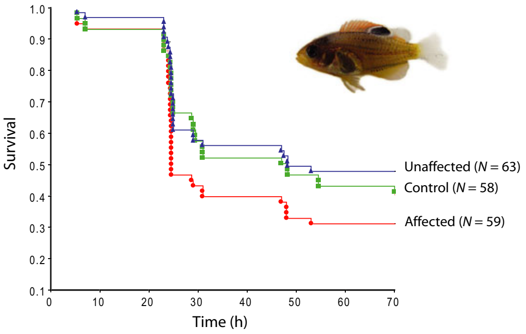

Figure 5 Selective mortality in juvenile damselfish exposed to elevated CO_2. Juvenile fish were exposed to elevated (700 μatm) or control (425 μatm) CO_2 for 4 days. The behavioural sensitivity of each fish to high CO_2 was then tested in a two-channel flume, by presenting them with the olfactory cue of a predator. Individual fish were classified as either 'unaffected' (i.e. they were repelled from predator cue) or 'affected' (abnormally attracted to predator) by high CO_2. Juvenile fish were transplanted to small patch reefs, and their survival was monitored for 3 days. Survival was higher among individuals that were unaffected by high CO_2 (blue line) compared with those that were behaviourally affected by high CO_2 (red line), and there was no difference in survival among individuals that were unaffected by high CO_2 (blue line) and those that had been exposed to control levels of CO_2 (green line).

Conservation and management implications

While it is clear that predicted future warming and pCO_2 levels will have impacts on reef fish populations and communities, there is also evidence that these impacts could be moderated by acclimation and adaptation. The degree to which acclimation and adaptation will counter the impacts of rapid climate change over the next 50–100 years remains unknown. However, there are a number of practical management options that could support the adaptive potential in reef fish populations. Most importantly, maintaining standing genetic variation within populations will maximize the potential for genetic adaptation to climate change. Genetic variation is generally correlated with population size (Frankham 1996), and therefore, management approaches that maintain large populations and prevent population decline could help maximize the adaptive potential (Munday *et al.* 2013a). Such approaches could include the use of marine protected areas, reductions in fishing pressure and mitigation of other stressors that affect the abundance of reef fishes. Fishing can also impose a strong directional selection on fish populations (Pandolfi 2009); therefore, managing fishing efforts may be some of the most effective means of maintaining genetic diversity for climate change adaptation. Low-latitude populations of reef fishes appear to be most vulnerable to the effects of ocean warming, and consequently, management options that maintain population sizes and reduce other stressors in these populations should be a priority.

Another major consideration in predicting the potential for coral reef fishes to adapt to future climate change is their reliance on coral reef habitat. Scleractinian corals, the builders of the reef matrix and providers of complex reef habitat, are highly susceptible to rising temperatures and ocean acidification (Hoegh-Guldberg and Bruno 2010). Temperatures just a few degrees above the summer average over extended periods can lead to mass coral bleaching and mortality. Calcification rates of corals are also sensitive to declining aragonite saturation state from ocean acidification (Kleypas and Yates 2009; Doney *et al.* 2012). The pCO_2 and temperature changes that would have significant effects on reef fishes (>600 μatm CO_2 and +2 °C) could have even more severe effects on coral reef habitat (Hoegh-Guldberg *et al.* 2007). Loss of coral cover and habitat structural complexity due to climate change will have significant effects on reef fish communities (Pratchett *et al.* 2008, 2015). Up to 75% of reef fish species may decline in abundance following severe habitat degradation, with some species declining in abundance by 50% or more (Jones *et al.* 2004). Consequently, habitat degradation from climate change is likely to have a more immediate impact on fish populations than the direct effects of rising temperatures and pCO_2. Management strategies that reduce other stressors on coral reefs, thereby enhancing their ability to absorb and recover from climate-related impacts, will help maintain healthy fish populations and thus their adaptive potential to the direct effects of rising temperatures and CO_2 levels.

Conclusions and future directions

Coral reef fishes had their origins in a geological time when CO_2 levels and temperatures were much higher than those in the current day. As a result, they possess some adaptations that could help them cope with projected future climate change, such as well-developed capacity for acid–base/ion regulation and maintaining oxygen delivery in a high CO_2 environment. However, extant coral reef fishes mostly diverged during the Pleistocene, when CO_2 levels and temperatures were similar to the present day; consequently, they are also adapted to the narrow temperature range of today's coral reef habitats. Temperatures of just 1.5–3 °C above current-day summer averages have significant effects on aerobic scope, swimming performance, growth and reproduction of most coral reef fishes tested to date, indicating their sensitivity to climate change. Furthermore, the uniformity of the thermal optimum for aerobic scope between equatorial and higher-latitude populations of reef fishes suggests that there has not been a strong local adaptation to thermal environments, at least in the species tested to date. As a result, equatorial populations appear to be living very close to their thermal limits for performance, and may suffer population declines, unless they can adapt to future warming. In contrast, higher-latitude populations may have a significant buffer against future warming because they are living at temperatures below their thermal optimum.

Elevated CO_2 does not appear to have a consistently negative effect on the physiology or life-history traits of most reef fishes tested to date. The low sensitivity of physiological processes to elevated CO_2 is likely to be associated with the well-developed mechanisms for acid–base/ion regulation in a high CO_2 environment exhibited by marine fishes. An unexpected finding, however, is the high sensitivity of sensory systems and behaviour of coral reef fishes to pCO_2 levels projected to occur in the second half of this century. These behavioural changes appear to be related to the effect of acid–base-relevant ion gradients on the function of GABA-A neurotransmitter receptors. Consequently, the physiological mechanisms that enable reef fishes to regulate pH under elevated environmental CO_2 may ultimately lead to behavioural impairment.

Reef fishes appear to have the limited capacity for reversible acclimation, probably because they are adapted to an environment with relatively low seasonal variability; however, new studies have revealed a considerable capacity for developmental and transgenerational thermal acclimation. These forms of plasticity could enable reef fishes to persist and adjust to a future warmer environment. However, not all traits exhibit equal plasticity. For example, the effects of elevated CO_2 on reef fish behaviour are not mitigated by the exposure of several generations to the same environment. In this case, genetic adaptation will be required to overcome the negative effects of rising CO_2 levels on fish neurophysiology and behaviour.

Studies on the potential of marine fishes to adapt to future higher temperatures and CO_2 levels are in their infancy. Research into genetic variation and the heritability of phenotypic traits that are sensitive to elevated temperature and pCO_2 in reef fishes is desperately needed. Short-term exposures to high temperatures and pCO_2 can demonstrate acute sensitivity to these environmental drivers, but such experiments are unlikely to provide an accurate representation of future population responses due to the combined effects of plasticity and adaptation. Further research on these topics is a priority. Well-established methods exist for estimating genetic variation and heritability, but difficulties in closing the life cycle of most broadcast-spawning reef fishes and constraints imposed by the breeding system of demersal-spawning reef fishes pose challenges to this research programme. Nevertheless, a range of different methods are possible and novel approaches must be tried. Variation in evolutionary potential among species and populations is certain to occur. An important goal will be to predict which species and populations have the greatest potential to adapt to climate change and which species and populations are most vulnerable. Ultimately, only with an evolutionary perspective can we hope to reliably predict the impacts of these stressors on reef fish populations and coral reef communities.

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