

COMMENTARY

Impact of global warming and rising CO₂ levels on coral reef fishes: what hope for the future?

Philip L. Munday^{1,*}, Mark I. McCormick¹ and Göran E. Nilsson²

¹ARC Centre of Excellence for Coral Reef Studies, and School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia and ²Physiology Programme, Department of Molecular Biosciences, University of Oslo, 0316 Oslo, Norway

*Author for correspondence (Philip.Munday@jcu.edu.au)

Summary

Average sea-surface temperature and the amount of CO₂ dissolved in the ocean are rising as a result of increasing concentrations of atmospheric CO₂. Many coral reef fishes appear to be living close to their thermal optimum, and for some of them, even relatively moderate increases in temperature (2–4°C) lead to significant reductions in aerobic scope. Reduced aerobic capacity could affect population sustainability because less energy can be devoted to feeding and reproduction. Coral reef fishes seem to have limited capacity to acclimate to elevated temperature as adults, but recent research shows that developmental and transgenerational plasticity occur, which might enable some species to adjust to rising ocean temperatures. Predicted increases in P_{CO₂}, and associated ocean acidification, can also influence the aerobic scope of coral reef fishes, although there is considerable interspecific variation, with some species exhibiting a decline and others an increase in aerobic scope at near-future CO₂ levels. As with thermal effects, there are transgenerational changes in response to elevated CO₂ that could mitigate impacts of high CO₂ on the growth and survival of reef fishes. An unexpected discovery is that elevated CO₂ has a dramatic effect on a wide range of behaviours and sensory responses of reef fishes, with consequences for the timing of settlement, habitat selection, predator avoidance and individual fitness. The underlying physiological mechanism appears to be the interference of acid–base regulatory processes with brain neurotransmitter function. Differences in the sensitivity of species and populations to global warming and rising CO₂ have been identified that will lead to changes in fish community structure as the oceans warm and becomes more acidic; however, the prospect for acclimation and adaptation of populations to these threats also needs to be considered. Ultimately, it will be the capacity for species to adjust to environmental change over coming decades that will determine the impact of climate change on marine ecosystems.

Key words: thermal reaction norm, aerobic scope, hypoxia, ocean acidification, acid–base regulation, olfaction, behaviour, population viability, range shift, acclimation, adaptation, climate change.

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Introduction

The concentration of CO₂ in the atmosphere has increased from approximately 280 p.p.m. at the start of the industrial revolution to over 390 p.p.m. now as a result of fossil fuel burning, cement production and land use changes (IPCC, 2007; Peters et al., 2012). This increase in atmospheric CO₂ has caused Earth's average surface temperature to increase by approximately 0.7°C. Depending on the magnitude of future CO₂ emissions, average surface temperature is projected to rise another 2–4°C by the year 2100 (IPCC, 2007). Tropical ecosystems are predicted to be especially sensitive to global warming because many tropical species appear to have a narrow thermal tolerance range, possibly as a result of having evolved in a relatively stable thermal environment (Deutsch et al., 2008; Tewksbury et al., 2008; Wright et al., 2009). Consequently, even relatively small increases in temperature could exceed the thermal optimum for some tropical species, leading to declines in individual performance that could affect population sustainability, community structure and ecosystem function. In the ocean, coral reefs are considered to be especially vulnerable to global warming because many coral species live within 1–2°C of their critical thermal limits (Hoegh-Guldberg et al., 2007). While loss of living coral habitat would

affect the distribution and abundance of many reef-associated species (Pratchett et al., 2008; Pratchett et al., 2009), there will also be direct effects of rising temperature on these organisms. Not all coral reef organisms are as thermally sensitive as corals, and how they will fare in a warmer world will depend on how close they are living to their thermal optimum and what capacity they have to acclimate and adapt to rising temperatures over the coming decades (Munday et al., 2008a; Franklin and Seebacher, 2009; Wilson et al., 2010). Because of the air–sea equilibrium, CO₂ concentrations in the surface ocean are also increasing (Doney, 2010), and although the potential impacts of elevated CO₂ are less well known for most marine organisms, they might nevertheless be significant and could interact with rising temperature (Pörtner et al., 2005; Pörtner and Farrell, 2008).

In water-breathing animals such as fish, a mismatch between increasing oxygen demand at higher temperatures and the capacity of the circulatory and ventilatory systems to supply oxygen to tissues is thought to be associated with thermal tolerance (Fry, 1947; Pörtner and Knust, 2007; Pörtner and Farrell, 2008). According to this hypothesis, the scope for aerobic performance will decline above the optimal temperature range, with consequences for activity levels, growth rate, reproduction and,

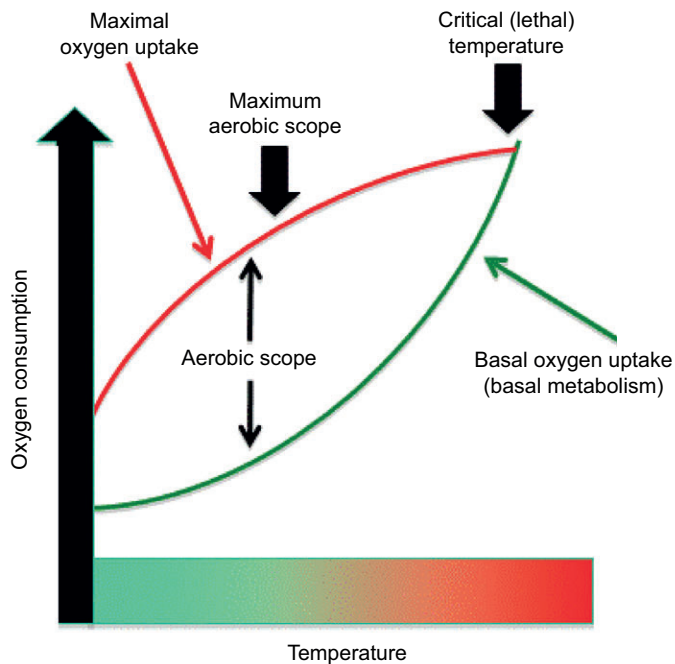


Fig. 1. Aerobic scope is the difference between the minimum rate of oxygen consumption in unfed animals at rest and the maximum rate of oxygen consumption. Above (and below) a certain temperature, the aerobic scope will decrease. As temperature rises further, less energy can be devoted to processes like feeding and reproduction, thereby reducing the fitness of the animal. The critical (lethal) temperature is reached when the maximum capacity for oxygen uptake is needed just to supply basal oxygen needs.

ultimately, population survival (Fig. 1) [for a detailed discussion, see also Farrell (Farrell, 2009)]. Aerobic scope could be further affected by stressors such as elevated CO_2 , which might increase aerobic demand or suppress the efficiency of oxygen supply (Pörtner and Farrell, 2008). Because of the link between aerobic scope and individual performance (e.g. Pörtner and Knust, 2007; Farrell et al., 2008; Eliason et al., 2011), knowledge of thermal reaction norms of aerobic scope could provide valuable insights into the sensitivity of different species to global warming and the likely effects of interacting stressors such as ocean acidification. By comparing thermal reaction norms it may be possible to predict which species and populations are likely to be most sensitive to future increases in temperature and the interacting effects of rising CO_2 levels (Nilsson et al., 2009). Aerobic scope might also be useful for testing and comparing the capacity for species and populations to acclimate or adapt to rapid climate change, either by comparisons of aerobic scope from natural populations living under different environmental conditions (Eliason et al., 2011; Gardiner et al., 2010) or in long-term experiments under conditions consistent with future climate change predictions (Donelson et al., 2012).

Aerobic capacity in a warming ocean

Experimental evidence indicates that, as predicted, coral reef fishes live close to their thermal optimum, and that small increases in temperature can significantly reduce aerobic scope (Nilsson et al., 2009; Johansen and Jones, 2011); however, there is considerable variation among species. Nilsson et al. (Nilsson et al., 2009) found that two species of coral reef cardinalfish (family Apogonidae) were especially sensitive to increases in temperatures above the

summer average they usually experience (29°C). Aerobic scope of the two cardinalfishes was reduced by nearly half at 31°C compared with 29°C , and virtually all capacity for additional oxygen consumption was lost by 33°C . Cardinalfishes began dying after 8 days at 32°C (Nilsson et al., 2010), indicating that this temperature is beyond that at which even short-term persistence (i.e. days) is possible. In contrast, three damselfish species (Pomacentridae) retained over half their aerobic scope at 33°C compared with 29°C , and did not exhibit increased mortality. Variation in aerobic capacity has also been observed among damselfish species, with five of 10 species tested by Johansen and Jones (Johansen and Jones, 2011) exhibiting a reduction in aerobic scope from 29 to 32°C , but another five species exhibiting no significant change. Together, these results demonstrate that some coral reef fishes are sensitive to small increases in average summer temperature, but that the effects are much more dramatic in some species than others.

Reduced aerobic scope at elevated temperatures is also correlated with a reduction in hypoxia tolerance. Again using cardinalfish and damselfish, Nilsson et al. (Nilsson et al., 2010) showed that there was a positive correlation between resting oxygen consumption (\dot{M}_{O_2}) and the minimum oxygen content in water at which \dot{M}_{O_2} can be maintained (the critical oxygen level, $\text{O}_{2\text{crit}}$). As expected, both \dot{M}_{O_2} and $\text{O}_{2\text{crit}}$ increased with increasing water temperature in the cardinalfish *Ostorhinchus doederleini* and the damselfish *Pomacentrus moluccensis*, implying reduced hypoxia tolerance in warmer water. Consistent with the earlier findings, both variables increased more sharply in the cardinalfish than in the damselfish. The Q_{10} (an index for the rate of rise in \dot{M}_{O_2} with temperature) of the cardinalfish over the tested temperature range ($29\text{--}32^\circ\text{C}$) was 6.1, whereas the damselfish had a Q_{10} of 2.2. Correspondingly, $\text{O}_{2\text{crit}}$ increased by 71% in the cardinalfish, but only by 23% in the damselfish from 29 to 32°C (Nilsson et al., 2010). The predicted loss of hypoxia tolerance indicated by the increase in $\text{O}_{2\text{crit}}$ could have important consequences for reef fishes, because many of them shelter among coral branches, in crevices or within the reef matrix to avoid nocturnal predators (Nilsson and Östlund-Nilsson, 2004; Nilsson et al., 2007). Especially in lagoonal environments, these habitats can become severely hypoxic at night as a result of respiration of reef organisms, and therefore may provide less suitable refuges to fishes with a reduced hypoxia tolerance in a warmer future (Ohde and van Woesik et al., 1999; Nilsson et al., 2004; Clavier et al., 2008).

The difference in sensitivity of cardinalfishes and damselfishes to elevated temperatures described above has important ecological ramifications. Because of their higher sensitivity to increased temperature, cardinalfishes are predicted to exhibit rapid range shifts in response to global warming (Nilsson et al., 2009). As sea surface temperatures increase, low-latitude populations will become less viable. At the same time, high-latitude locations will become more suitable for population persistence, especially as overwintering temperatures exceed minimum thermal limits (Figueira and Booth, 2009). As a result of changes in locations where populations can persist, geographic distributions will shift to match the preferred thermal range. Damselfish populations may also shift toward higher latitudes, but the rate will be slower, and high-latitude populations are more likely to persist because of their greater thermal tolerance. As a result, the composition of low-latitude reef fish communities will change as thermally sensitive species experience local extinctions and more thermally tolerant species persist. At the same time, changes in fish community structure

will also occur in high-latitude locations due to range extensions and colonization of new areas by tropical species.

Reduced aerobic capacity at elevated temperature is expected to have significant implications for individual performance (Pörtner and Farrell, 2008). Reductions in aerobic scope at 32°C compared with 29°C in five species of damselfish was associated with a 21–28% reduction in critical swimming speed (Johansen and Jones, 2011). Importantly, comparisons with field conditions indicate that a reduction in swimming speed of this magnitude would leave some of these species unable to swim against the currents commonly found in their reef habitats. Laboratory experiments have demonstrated that increases of just 1.5–3°C in water temperature above summer averages lead to declines in somatic growth (Munday et al., 2008b) and reproductive performance (Donelson et al., 2010) of the coral reef damselfish *Acanthochromis polyacanthus*. Temperature increases of this magnitude cause complete cessation of reproduction in fish on a moderate ration diet and ~50% reduction in the number of active breeding pairs on a high ration diet (Donelson et al., 2010). Even on the high ration diet, the number of eggs laid per clutch, egg size and offspring size were all smaller for fish kept at the warmer temperatures. Unseasonally high water temperatures due to El Niño conditions have also been associated with recruitment failures of coral reef fishes in the central Pacific (Lo-Yat et al., 2011), possibly due to reproductive failure of adults at high temperatures. Reduced growth and reproductive output by *A. polyacanthus* at elevated temperatures is correlated with a sharp decline in aerobic scope at these temperatures (Donelson et al., 2012), suggesting that less energy is available for activities other than basic maintenance at higher temperatures. However, steroid hormones involved in reproduction are also temperature sensitive (Pankhurst and Munday, 2011) and the relative importance of these two physiological factors in explaining reproductive declines in reef fishes at elevated temperature remains unknown.

Increased temperature can also influence development and life history traits of larval reef fishes. There is ample evidence that higher temperatures (within the natural range) accelerate development, increase growth rate, and reduce the pelagic duration of larval coral reef fishes (McCormick and Molony, 1995; Meekan et al., 2003; Green and Fisher, 2004; Sponaugle et al., 2006). The ecological impact of such changes are still poorly understood, but could include improved survival rates due to shorter duration in the pelagic environment (O'Connor et al., 2007), more variable survival due to a greater risk of starvation associated with increased metabolic rate, and reduced dispersal distances due to reduced time in the pelagic stage (Munday et al., 2009a). Experimental studies are now required that test the early life history traits of coral reef fish larvae at temperatures above the present-day range experienced in nature, to determine if the rate of larval developmental continues to increase at temperatures consistent with global warming predictions, or if they too are operating close to their thermal optimum and exhibit a decline in performance at elevated temperatures.

The potential for thermal acclimation and adaptation

Tropical species are often predicted to have limited capacity for thermal acclimation because they have evolved in a relatively stable thermal environment (Stillman, 2003; Tewksbury et al., 2008). To date, only a handful of studies have examined thermal acclimation in coral reef fishes, but all indicate that adult fish have limited capacity for acclimation to increasing temperature (e.g. Nilsson et al., 2010). For example, *Pomacentrus moluccensis* kept for 22 days

at 32°C did not exhibit improved aerobic capacity compared with fish kept for 0 or 7 days at this temperature (Nilsson et al., 2010). Similarly, breeding pairs of *A. polyacanthus* continue to experience significant decrements in reproductive performance even after months of exposure to elevated temperature (Donelson et al., 2010). These results suggest that future generations of these species will suffer significant impacts from increasing ocean temperatures.

However, there is exciting new evidence for developmental and transgenerational acclimation to elevated temperature in coral reef fishes. *Acanthochromis polyacanthus* reared from hatching at 3°C above present-day summer averages exhibit a smaller increase in resting metabolic rate compared with fish reared at present-day averages and tested at elevated temperatures (Donelson et al., 2011). Furthermore, when these developmentally acclimated fish are reared to adulthood, and their offspring are then reared at elevated temperature, the offspring exhibit a remarkable increase in aerobic scope compared with fish that have not been acclimated to elevated temperatures for several generations (Donelson et al., 2012). The aerobic scope of fish reared at +1.5 and +3°C above present-day temperatures returns to present-day control levels within two generations (Fig. 2). These new studies demonstrate that despite having little capacity for reversible acclimation as adults, some coral reef fishes have considerable capacity for transgenerational thermal acclimation. This has important consequences for climate change research, because the full potential to cope with rising ocean temperature may take several generations to be expressed.

The mechanisms responsible for the dramatic improvement in aerobic performance between generations observed by Donelson et al. (Donelson et al., 2012) are yet to be identified, but could be associated with variation in epigenetic state (Jablonka and Raz, 2009). Specifically, changes in gene expression and cellular

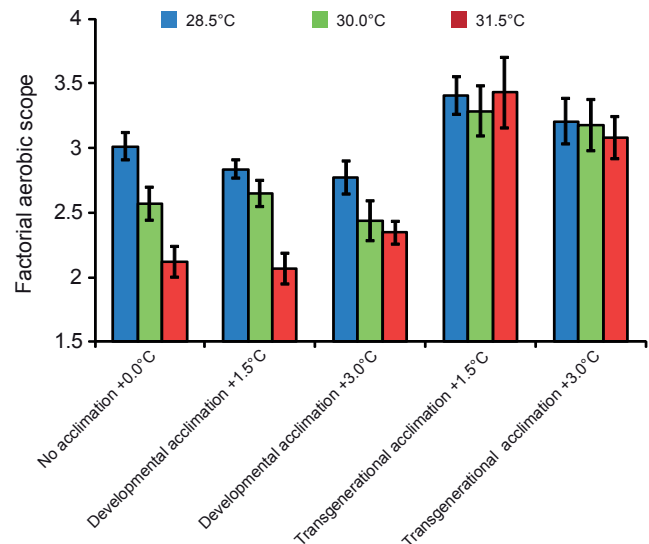


Fig. 2. Aerobic scope in juvenile spiny damselfish *Acanthochromis polyacanthus* at 28.5, 30.0 and 31.5°C for different thermal acclimation groups. Aerobic scope declined at 30.0 and 31.5°C in juvenile fish that were reared from hatching at 28.5°C (no acclimation group). Rearing from hatching at elevated temperature did not significantly increase aerobic scope (developmental acclimation). However, aerobic scope was fully restored in juvenile fish at 30.0 and 31.5°C when the parental generation also experienced the elevated temperatures their whole life (transgenerational acclimation groups). From Donelson et al. (Donelson et al., 2012).

function of parents exposed to elevated temperature may prime their offspring to develop more efficient physiological pathways for a warmer environment. Non-genetic inheritance is a rapidly emerging field of biological and evolutionary study (Bonduriansky, 2012), with numerous examples of the environmental conditions experienced in one generation having important consequences for future generations (Jablonka and Raz, 2009). Theory predicts that such effects could be critically important to the adaptation of species to a rapidly changing climate (Bonduriansky et al., 2012). It is surprising, therefore, that more attention has not been given to this topic in climate change research and we suggest that it will be an important area for future experimental investigation.

Despite the prospect of greater capacity for thermal acclimation in reef fishes than previously expected, it should also be recognized that acclimation may incur some costs or involve trade-offs with other traits (Angilletta et al., 2003). For example, thermally acclimated fish were smaller than non-acclimated fish in the experiments conducted by Donelson et al. (Donelson et al., 2011; Donelson et al., 2012), suggesting that physiological acclimation

might have some energetic cost that reduces the energy available for somatic growth. Consequently, future studies on transgenerational acclimation also need to consider the potential implications for growth, fecundity and other life history traits.

Although local populations of coral reef fishes may be sensitive to small increases in water temperature, many species also have large geographic ranges that span temperature gradients greater than projected changes in ocean temperature due to global warming (Munday et al., 2008a). The occurrence of populations across such temperature gradients illustrates that many species must possess the capacity for local thermal acclimation and adaptation, even if adults exhibit little capacity for within-generation acclimation. In one of the only comparative studies conducted to date for coral reef fishes, Gardiner et al. (Gardiner et al., 2010) found that high-latitude populations exhibited similar or higher aerobic scope than low-latitude populations of the same species when tested at the temperatures inhabited by the low-latitude population, and at temperatures up to 4°C above the summer average (Fig. 3). This counter-gradient

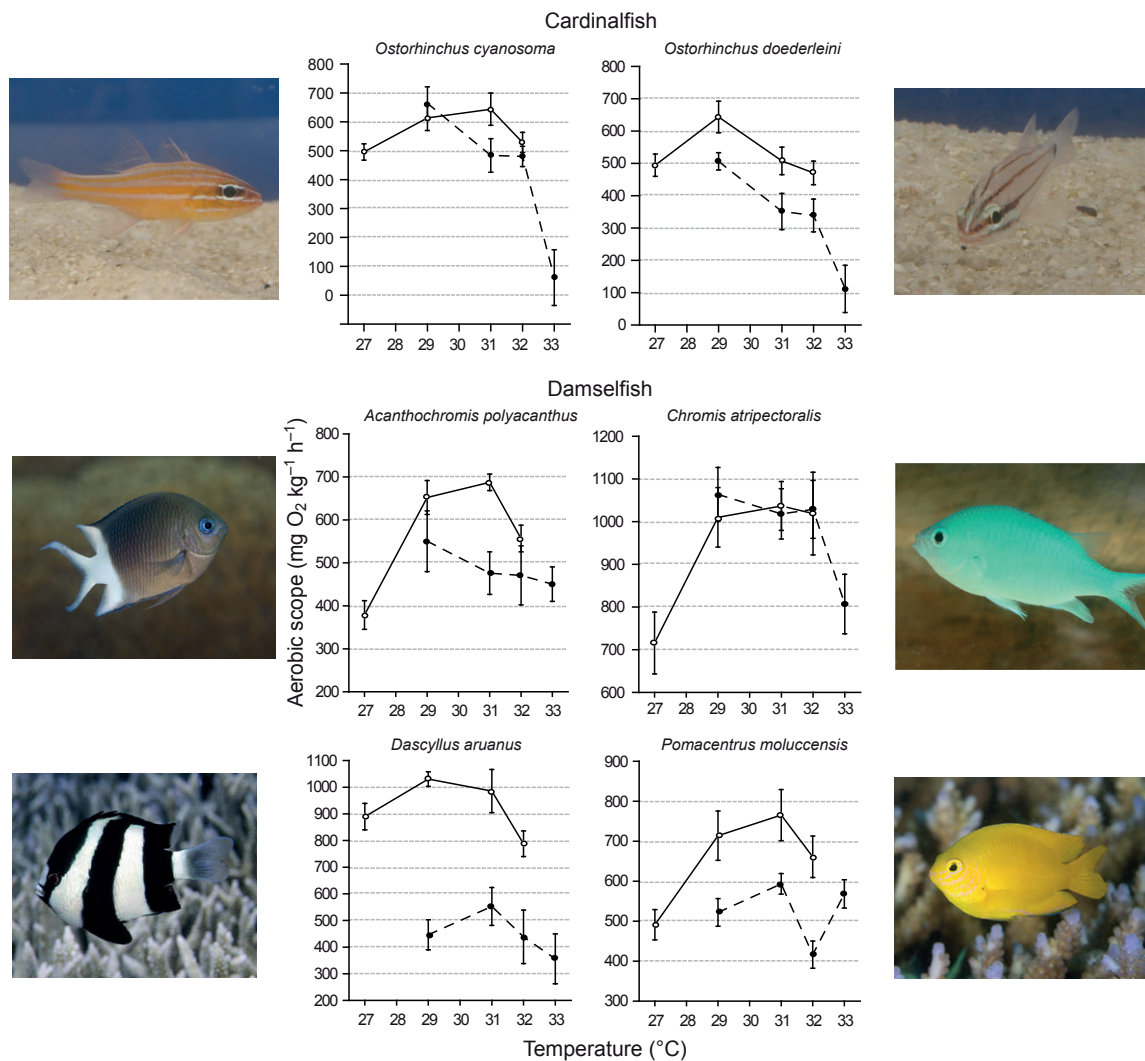


Fig. 3. Aerobic scope varies between populations in four out of six tested species of cardinalfishes and damselfishes from Heron Island (solid lines) and Lizard Island (dashed lines). In general, the populations from Heron Island have a higher aerobic scope at a particular temperature than those from Lizard Island, even though Lizard Island is >1200 km closer to the equator and has a warmer average summer temperature than Heron Island (28.9°C versus 27.5°C). Larger seasonal variations in temperature further from the equator may explain this countergradient variation. It may also reflect compensation in respiratory performance to allow for a high aerobic scope even at a relatively low water temperature. From Gardiner et al. (Gardiner et al., 2010). Photo credits: J. Krajewski, I. Lunde, R. Patzner and G.E.N.

variation in aerobic capacity suggests that high-latitude populations are locally acclimated or adapted to the greater variation in temperature they experience compared with low-latitude populations. This acclimation or adaptation to temperature variation could enable them to perform better at temperatures above their summer average compared with low-latitude populations. Similar counter-gradient patterns of thermal preference and tolerance have been observed in temperate fishes (Fangue et al., 2009; Baumann and Conover, 2011). For coral reef fishes, the counter-gradient variation in aerobic capacity was mostly driven by high-latitude populations exhibiting up to 80% higher maximum rates of oxygen consumption ($\dot{M}_{O_2, \max}$) compared with low-latitude populations. The adaptive advantage of a higher $\dot{M}_{O_2, \max}$ in high-latitude populations is currently unknown, but could be related to a need for increased aerobic scope to offset detrimental effects of cooler water on one or more life history traits. In particular, increased metabolic rate could help maintain growth and developmental rates in cooler water, as observed in many temperate fishes (Conover et al., 2009).

Elevated CO₂ and aerobic scope

The effects of rising atmospheric CO₂ on marine fishes have received much less attention than those of rising temperature. This is possibly because adult fish are known to closely regulate their acid–base balance (Claiborne et al., 2002; Brauner and Baker, 2009) and previous studies have indicated that the CO₂ levels that cause mortality in adult fish are often an order of magnitude or more higher (>10,000 μatm) (Ishimatsu et al., 2008) than the CO₂ levels predicted for the atmosphere and surface ocean by the end of this century (up to ~1000 μatm under a business-as-usual scenario of CO₂ emissions). Nevertheless, fishes are sensitive to increasing environmental CO₂ because the CO₂ of body fluids is often relatively close to ambient conditions [just a few mmHg above ambient in some species (Evans et al., 2005)]. Consequently, even relatively small increases in ambient CO₂ can lead to increases in plasma P_{CO_2} . Very high concentrations of environmental CO₂ (>10,000 μatm) are known to affect respiration, circulation and metabolism of some fishes (Ishimatsu et al., 2005); however, the effects of the more moderately increased CO₂ concentrations projected to occur in the surface ocean this century, and the associated changes in seawater pH, are only just starting to be

explored. In one of the first studies conducted to date, Munday et al. (Munday et al., 2009b) found that exposure to ~1000 μatm CO₂ reduced aerobic scope by 33–47% in the same two species of cardinalfishes that were observed to be highly sensitive to elevated water temperature in the other studies mentioned above (Nilsson et al., 2009; Gardiner et al., 2010). The effect of 1000 μatm CO₂ on aerobic performance was similar to a 4°C increase in temperature in both species, and in *Ostorhinchus doederleini* caused an increase in mortality at 32–33°C, which appears to be close to the critical thermal limit for this species (Nilsson et al., 2010). In contrast, Rummer et al. (Rummer et al., in revision) found that $\dot{M}_{O_2, \max}$ and therefore aerobic scope of adult *A. polyacanthus* increased by 38% when exposed to ~1000 μatm CO₂ for 2 weeks. These two studies, both conducted at the same location, indicate that the effects of near-future CO₂ levels on oxygen uptake can vary markedly among coral reef fish species. Understanding this variation will be important for predicting the effects of climate change on coral reef fish communities, because for some species elevated CO₂ levels may exacerbate the effects of ocean warming on aerobic scope, leading to rapid population decline, whereas in other species, elevated CO₂ levels might mitigate the effects of warmer temperatures.

The effects of elevated CO₂ levels on reef fish life history traits are also highly variable. Near-future CO₂ levels had no effect on growth rate of juvenile *A. polyacanthus* (Munday et al., 2011), tended to increase growth rate of larval clownfish, *Amphiprion percula* (Munday et al., 2009c), but had a negative effect on growth rate of the anemonefish *Amphiprion melanopus* (Miller et al., 2012). Importantly, parental effects have been found to dramatically modify the response of juvenile reef fish to elevated CO₂ levels, just as they do for elevated temperature. Growth and survival decreased in juvenile *A. melanopus* reared for 3 weeks at 1000 μatm CO₂; however, these effects were absent in juveniles whose parents were also reared under high CO₂ (Miller et al., 2012). Due to concerns about the potential effects of ocean acidification, there has been a recent surge in research on effects of near-future CO₂ levels and reduced pH on fish and other marine organisms (Gattuso and Hansson, 2011). The new results from Miller et al. (Miller et al., 2012) demonstrate that ocean acidification studies will need to consider the potential for marine species to adjust their physiological responses to elevated CO₂

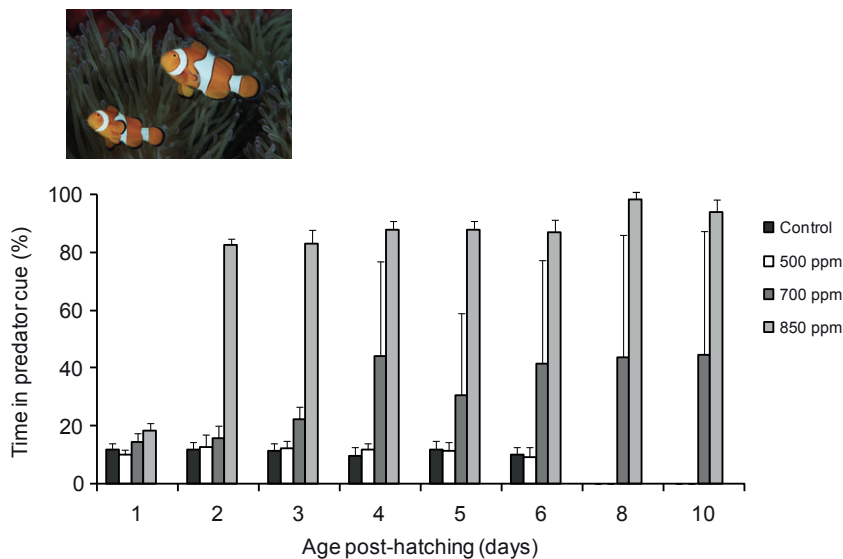


Fig. 4. Exposure to elevated CO₂ levels affects olfactory preferences in larval reef fishes. Larval clownfishes reared from hatching at control (~390 μatm) or 500 μatm CO₂ exhibit a strong avoidance of predator odour. In contrast, clownfishes reared at 700 or 850 μatm CO₂ develop a strong preference for predator odour after 4 and 2 days, respectively. Clownfish were exposed to control, 550, 700 or 850 μatm CO₂ from hatching, and their behavioural responses were assessed at regular ontogenetic stages using a flume chamber where they could freely move between a stream of water containing the predator cue and a stream of water without the cue. Shown is mean (\pm s.d.) time that clownfish larvae spent in the stream of water containing the predator odour. Reproduced with permission from Munday et al. (Munday et al., 2010). Photo credit: S. Foale.

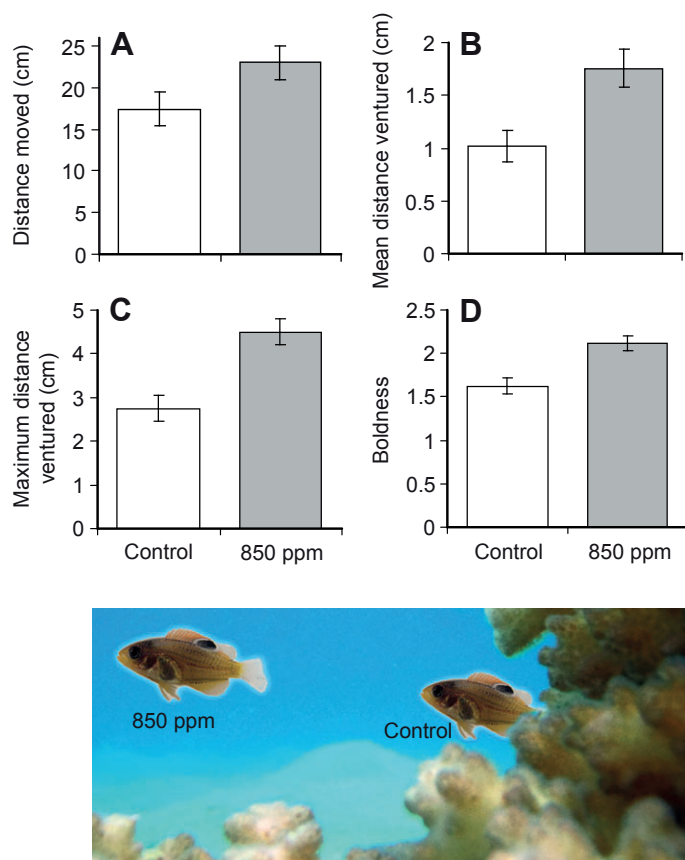


Fig. 5. The behaviour of larval reef fish is altered by exposure to elevated CO_2 levels. When placed in natural coral reef habitat, juvenile damselfish exposed to $850 \mu\text{atm CO}_2$: (A) were more active, (B) ventured further from shelter, (C) ventured a greater maximum distance from shelter and (D) were bolder (on a scale of 0 to 3 with 0.5 increments) compared with juveniles exposed to present-day CO_2 levels. Damselfish were caught in light traps at the end of their pelagic larval phase and exposed to control or to $850 \mu\text{atm CO}_2$ for 4 days. They were then released onto patches of coral habitat and their behaviour was observed. From data published in Munday et al. (Munday et al., 2010).

levels when several generations are exposed to the same environmental stress.

Sensory and behavioural abnormalities – the greatest threat of rising CO_2 levels?

A major development in understanding the impacts of rising CO_2 levels on marine organisms was the discovery that exposure to elevated CO_2 levels affects the behaviour and sensory responses of coral reef fishes. Initial studies showed that juvenile damselfish exposed to elevated CO_2 levels became more active (Munday et al., 2010) and lost their ability to discriminate between ecologically important chemical cues, such as odours from different habitat types, kin and non-kin, and the smell of predators (Munday et al., 2009d; Dixon et al., 2010). Remarkably, the high- CO_2 -exposed juveniles even became strongly attracted to the smell of a predator (Fig. 4). Reef fish larvae use olfactory cues to help locate reefs at the end of their pelagic larval phase, to choose appropriate settlement habitat and to avoid predators (Leis et al., 2011). Consequently, impaired ability to discriminate between olfactory cues, or attraction to inappropriate cues, could have serious consequences for the ability of larvae to locate reefs and

successfully transition from the pelagic to the benthic environment. Subsequent studies have found that effects of near-future CO_2 levels are not restricted to olfactory-mediated behaviour; auditory preferences (Simpson et al., 2011), behavioural lateralization (Domenici et al., 2012), learning ability (Ferrari et al., 2012a) and visual threat perception (Ferrari et al., 2012b) are all affected when juvenile reef fishes are exposed to elevated CO_2 levels. These impacts on behaviour and sensory systems have been shown to affect homing ability (Devine et al., 2012a), habitat selection and the timing of settlement (Devine et al., 2012b), predator avoidance (Ferrari et al., 2011a) and prey selection (Ferrari et al., 2011b). Furthermore, juvenile damselfish exposed to elevated CO_2 levels ($700\text{--}850 \mu\text{atm CO}_2$) exhibit riskier behaviour in natural coral reef habitat, including higher activity levels and venturing further from shelter (Fig. 5). As a result, mortality from predation is five to nine times higher than average in newly settled juveniles that have been exposed to elevated CO_2 levels (Munday et al., 2010; Ferrari et al., 2011a). Such dramatic increases in mortality could clearly have implications for the sustainability of some reef fish populations.

Interference of acid–base regulatory responses with the function of brain neurotransmitters appears to be responsible for the systemic effects of high CO_2 levels on behaviour and sensory function observed in reef fishes (Nilsson et al., 2012). When exposed to high CO_2 levels, marine fish regulate their acid–base balance to avoid acidosis by accumulating HCO_3^- , with compensatory reductions in Cl^- (Brauner and Baker, 2009). The GABA-A receptor, the main inhibitory neurotransmitter receptor in the vertebrate brain, is an ion channel with conductivity for Cl^- and HCO_3^- (Bormann et al., 1987). Consequently, regulatory changes in the distribution of HCO_3^- and Cl^- over neuronal membranes during high- CO_2 exposure could affect GABA-A receptor function, and explain changes and reversals in behavioural responses (Fig. 6). By treating juvenile fish with an antagonist to the GABA-A receptor, Nilsson et al. (Nilsson et al., 2012) were able to reverse the behavioural abnormalities caused by CO_2 exposure, providing support for a role of impaired neurotransmitter function in the behavioural and sensory changes observed in reef fish at near-future CO_2 levels. Ironically, it seems that the exceptional capacity that marine fishes have to regulate their acid–base balance to prevent plasma and tissue acidosis could make them susceptible to behavioural and sensory impairment when permanently exposed to high CO_2 levels.

As observed with sensitivity to thermal stress, striking differences in the responses of different species to elevated CO_2 levels has been detected. In a comparison of four closely related damselfish species, Ferrari et al. (Ferrari et al., 2011a) found that all four species exhibited a reduced response to predation risk following exposure to high CO_2 levels, but the magnitude of the change ranged from 30 to 95%. Such differences suggest that the composition of reef fish communities may shift due to changes in relative rates of mortality among species in a high- CO_2 world. Whether reef fish will be able to acclimate or adapt to the effects of high concentrations of CO_2 on neurotransmitter function is currently unknown. At present, there is little evidence that developmental acclimation will play a major role in allowing future populations to cope with the behavioural and sensory impacts of increasing CO_2 , because behavioural changes occur in larvae even when they have been reared from hatching at elevated CO_2 levels (Munday et al., 2009d; Munday et al., 2010). Nevertheless, there is some hope that adaptation by selection of tolerant genotypes may occur. Although all tested damselfish larvae exposed to $850 \mu\text{atm}$

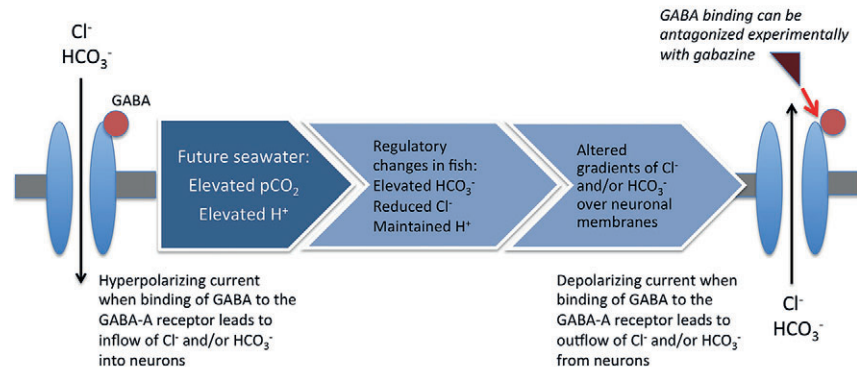


Fig. 6. Proposed response of GABA-A receptor function to elevated seawater CO₂ levels. GABA is the major inhibitory neurotransmitter in vertebrates. The GABA-A receptor is a GABA-gated ion channel with conductance for Cl⁻ and HCO₃⁻. Normally, ion gradients are such that channel opening results in Cl⁻ and HCO₃⁻ inflow, causing membrane hyperpolarization and inhibited neural activity. Elevated seawater P_{CO₂} leads to ion-regulatory adjustments in blood and tissues of fish that might affect transmembrane gradients for Cl⁻ and/or HCO₃⁻ in some neurons. This could cause GABA-A receptors to become depolarizing and excitatory, resulting in behavioural abnormalities. Nilsson et al. (Nilsson et al., 2012) provided support for this hypothesis by showing that the behavioural effects of high CO₂ exposure are reversed by treatment with a GABA-A receptor antagonist. From Nilsson et al. (Nilsson et al., 2012).

CO₂ show altered preferences to olfactory cues, larvae reared at 700 μatm CO₂ exhibit considerable variation in their responses, with approximately half of the larvae responding like unaffected controls (Munday et al., 2010). If this variation in individual responses has a genetic basis, we might expect rapid selection of tolerant individuals, although they may not be able to cope with further rises in CO₂. Estimating the heritability of variation in responses to high CO₂ levels among individuals will be key to making predictions about how species will respond to future ocean conditions.

Conclusions

Coral reef fishes appear to be sensitive to both rising ocean temperatures and higher CO₂ levels. Although there are differences in thermal sensitivity among species, most species tested to date appear to live close to their thermal optimum and even small increases in average temperature cause significant decrements to aerobic scope, leading to declines in growth, reproductive output, swimming ability and, in some cases, survival. Low-latitude populations appear to be more sensitive to rising ocean temperature than higher-latitude populations, possibly because they are acclimated or locally adapted to a narrower range of seasonal temperature. Adult reef fishes appear to have limited capacity to acclimate to higher temperature. More promisingly, however, at least some species are able to acclimate essential physiological processes to higher temperatures when both parents and offspring are exposed to these conditions. CO₂ concentrations that will occur in the ocean during the second half of this century could also have significant impacts on reef fish populations. The most dramatic effects are on behaviour and sensory ability: navigation, habitat choice, prey selection and predator avoidance by reef fishes could all be affected, with important consequences for population dynamics. Understanding the variation within and between species in their response to increasing temperature and CO₂ levels will be crucial for predicting the community and ecosystem effects of climate change. Tolerant species are likely to persist in their current locations, whereas sensitive species might exhibit rapid range shifts, or even suffer population declines throughout their ranges. Furthermore, greater emphasis needs to be placed on long-term experiments when investigating climate change impacts, because there is clearly potential for acclimation within and between

generations and the capacity for adaptation by selection of favourable genotypes. Ultimately, it will be these longer-term processes that determine the fate of coral reef fish populations as the climate changes over the next 50 to 100 years.

Glossary

Acclimation

The modification of physiological, behavioural or morphological traits in response to environmental change. This definition follows Angilletta (Angilletta, 2009), where the phenotypic change of the organism, not simply the duration of exposure, is considered to be acclimation.

Aerobic scope

The difference between maximum and minimum oxygen consumption.

Counter-gradient variation

A pattern of reaction norms whereby populations from cooler locations outperform populations from warmer locations at most temperatures, including the temperature normally experienced at the warmer location. Predicted to occur when genetic and environmental influences on performance are negatively associated across the thermal gradient.

\dot{M}_{O_2}

The 'resting' or 'standard' rate of oxygen consumption. This measure is an attempt to estimate the basal metabolic rate and is measured in unstressed fish that are not digesting feed. 'M' denotes that the value is given as mass of oxygen consumed. When it is given as volume of oxygen consumed, it is often denoted \dot{V}_{O_2} .

$\dot{M}_{O_2,max}$

The maximum rate of oxygen uptake that can be achieved. To estimate this in fish, oxygen consumption is measured during swimming at the maximum rate they can sustain.

$O_{2,crit}$

The critical oxygen concentration. This is the lowest level of oxygen in the water needed by the fish to sustain its resting rate of oxygen uptake. A low value indicates a high capacity for maintaining oxygen uptake during hypoxic conditions. May also be given as critical oxygen pressure ($P_{O_{2,crit}}$).

Q_{10}

The increase in the rate of a physiological process (often referring to \dot{M}_{O_2}) over a 10°C increase in temperature.

Thermal reaction norm

The response of a trait, such as aerobic scope, to variation in environmental temperature.

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