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Intrageneric variation in antipredator responses of coral reef fishes affected by ocean acidification: implications for climate change projections on marine communities

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Abstract

Our planet is experiencing an increase in the concentration of atmospheric carbon dioxide (CO_2) unprecedented in the past 800 000 years. About 30% of excess atmospheric CO_2 is absorbed by the oceans, thus increasing the concentration of carbonic acid and reducing the ocean's pH. Species able to survive the physiological stress imposed by ocean acidification may still suffer strong indirect negative consequences. Comparing the tolerance of different species to dissolved CO_2 is a necessary first step towards predicting the ecological impacts of rising CO_2 levels on marine communities. While it is intuitive that not all aquatic species will be affected the same way by CO_2, one could predict that closely related species, sharing similar life histories and ecology, may show similar tolerance levels to CO_2. Our ability to create functional groups of species according to their CO_2 tolerance may be crucial in our ability to predict community change in the future. Here, we tested the effects of CO_2 exposure on the antipredator responses of four damselfish species (*Pomacentrus chrysurus*, *Pomacentrus moluccensis*, *Pomacentrus amboinensis and Pomacentrus nagasakiensis*). Although being sympatric and sharing the same ecology and life history, the four congeneric species showed striking and unexpected variation in CO_2 tolerance, with CO_2-induced loss of response to predation risk ranging from 30% to 95%. Using *P. chrysurus* as a model species, we further tested if these behavioural differences translated into differential ability to survive predators under natural conditions. Our results indicate that *P. chrysurus* larvae raised under CO_2 levels predicted by 2070 and 2100 showed decreased antipredator responses to risk, leading to a five- to sevenfold increase in predation-related mortality in the first few hours of settlement. Examining ocean acidification, along with other environmental variables, will be a critical step in further evaluating ecological responses to predicted climatic change.

Keywords: antipredator response, hypercapnia, interspecific variation, ocean acidification, Pomacentridae, survival

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Introduction

Increases in atmospheric carbon dioxide (CO_2) are causing global warming and ocean acidification (Houghton, 2004; The Royal Society, 2005), which have been identified as major causes of change in biological systems (Hoegh-Guldberg *et al.*, 2007; Fabry *et al.*, 2008; Portner & Farrell, 2008; Brierley & Kingsford, 2009). For the past 800 000 years, atmospheric CO_2 concentrations have ranged from 170 to 300 ppm (Luthi *et al.*, 2008), but the release of additional anthropogenic CO_2 since the industrial revolution has caused CO_2 concentrations to rise to present-day levels of approximately 380 ppm (Meehl *et al.*, 2007). Greenhouse gas emission scenarios predict that atmospheric CO_2 concentration could exceed 850 ppm by 2100 (Meehl *et al.*, 2007; Raupach *et al.*, 2007), with a rate of increase ~100 times faster than historical norms (The Royal Society, 2005; Hoegh-Guldberg *et al.*, 2007). Increased levels of atmospheric CO_2 translates into increased levels of dissolved CO_2 in the oceans, leading to two major reactions: (1) CO_2 reacting with water to generate carbonic acid, bicarbonate and hydrogen ions, which increases the acidity of the water, and (2) increasing hydrogen ions bonds with carbonate ions to form more bicarbonate, leading to a reduction in carbonate-ion saturation (Orr *et al.*, 2005; Fabry *et al.*, 2008). Increased levels of dissolved CO_2 can affect metabolic and developmental processes of some marine species (Kurihara, 2008; Rosa & Seibel, 2008;

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Widdicombe & Spicer, 2008) and decreased carbonate ions concentrations are known to reduce calcification rates of corals and other invertebrates that precipitate aragonite skeletons (Orr *et al*., 2005; Hoegh-Guldberg *et al*., 2007; Kleypas & Yates, 2009).

Intuitively, one can predict that not all aquatic species will be affected the same way by CO_2 (Langer *et al*., 2006; Melzner *et al*., 2009) and considering differences in how species respond to ocean acidification will be critical for predicting community and ecosystem level effects of this threat (Fabry *et al*., 2008; Doney *et al*., 2009). A few studies have demonstrated variability in physiological responses of different species of calcifiers to elevated levels of CO_2, although the species compared often belonged to different orders (Kurihara, 2008; Clark *et al*., 2009; Miller *et al*., 2009; Ries *et al*., 2009). At a smaller phylogenetic scale, however, one could predict that closely related species, sharing similar life histories and ecology, may show similar tolerance levels to CO_2. If that is the case, then we may be able to create functional groups of species according to their CO_2 tolerance, which could be crucial in our ability to predict community change in the future. Only one study compared the effects of elevated CO_2 on the physiology and calcification of two congeneric species of oysters, and reported marked difference in CO_2 tolerance (Parker *et al*., 2010). However, given that the two species have much different evolutionary histories (one was native and one was recently introduced to the habitat in focus), this difference may be expected.

Although fish appear to be relatively more tolerant to elevated CO_2 than many invertebrates (Portner *et al*., 2004; Ishimatsu *et al*., 2008; Melzner *et al*., 2009), recent studies have shown that some reef fish suffer olfactory impairment when exposed to elevated CO_2 (Portner *et al*., 2005; Melzner *et al*., 2009; Munday *et al*., 2009a; Dixson *et al*., 2010). Because under low visibility conditions (i.e., in highly complex or turbid habitats or at night), fishes rely heavily on their chemosensory ability to detect predators (Ferrari *et al*., 2010), this olfactory impairment can increase mortality at key life history stages (Munday *et al*., 2010). Whether the degree of olfactory impairment caused by elevated CO_2 varies among closely related species is currently unknown, but is critical for understanding how reef fish community structure may be impacted by ocean acidification and for assessing the risk of cascading effects on ecological processes mediated by fishes in marine ecosystems. Here, we exposed four congeneric damselfish species (*Pomacentrus chrysurus*, *Pomacentrus amboinensis*, *Pomacentrus moluccensis* and *Pomacentrus nagasakiensis*) to three CO_2 concentrations (390, 700 or 850 ppm CO_2). Following the CO_2 treatment, we tested the ability of each of them to respond to predation-related risk cues. We hypothesized that given the phylogenetic, ecological and life-historical similarities among the species (Wellington & Victor, 1989; Ohman *et al*., 1998), CO_2 would have similar effects on them. To test whether CO_2-induced alteration in antipredator responses measured in the laboratory had survival consequences in natural conditions, we maintained larval *P. chrysurus* under 390 (control), 700 or 850 ppm of CO_2, released them individually on the reef, recorded their behaviour and monitored their survival until we observed ~50% mortality across groups. We predicted that the difference in behaviour measured would translate into differential survival in the field. We chose *P. chysurus* as a model species, as they showed an intermediate level of tolerance to CO_2.

Materials and methods

Fish collection and CO_2 treatment

Experiments took place at the Lizard Island Research Station (14°40′S, 145°28′E), on the Great Barrier Reef, Australia, in November and December 2009. We used established protocols to capture and treat our fish with CO_2 (Munday *et al*., 2009a, 2010). Presettlement juveniles (16–21 days old) of *P. chrysurus*, *P. moluccensis*, *P. amboinensis* and *P. nagasakiensis* were caught overnight in light traps (Meekan *et al*., 2001) moored approximately 100 m off the reef at Lizard Island. Light traps collect these fish at or immediately before their arrival on the reef at the end of the planktonic larval stage (Meekan *et al*., 1993). Every morning, the juveniles collected in the traps were transferred to 35 L rearing aquariums that were either aerated with 390 ppm (current-day control), 728 ± 88 or 1008 ± 78 ppm CO_2-enriched air (Munday *et al*., 2009a; Dixson *et al*., 2010). Aeration with CO_2-enriched air produced dissolved CO_2 levels of approximately 700 and 850 ppm (see Munday *et al*., 2010 for more details). Seawater for the system was pumped directly from the ocean into 70 L sumps, where it was aerated with the same concentration of CO_2-enriched air as the rearing aquariums. Rearing aquariums received a continuous flow of water from their respective sump at approximately 225–250 mL min^{-1}. Water temperature averaged 27.6 °C ± 1.3 [standard deviation (SD)]. Young damselfishes were fed freshly hatched *Artemia nauplii* three times a day. The fish were treated for 4 consecutive days and then used in our experiment immediately after the treatment period was over. Damselfish juveniles treated with 700 and 850 ppm CO_2 retained their impaired behavioural responses for at least 48 h after being transferred back into control water (Munday *et al*., 2010).

Laboratory assessment of interspecific variation in CO_2 effects

In this behavioural experiment conducted in 20 L clear, plastic aquaria, we maintained each of four damselfish species (*P. chrysurus*, *P. amboinensis*, *P. moluccensis* and *P. nagasakiensis*) at three CO_2 levels (390, 700 and 850 ppm) for 4 days and then quantified their foraging, swimming activity and microhabitat use before and after exposure to the odour of injured conspecifics, a reliable cue of general predation risk (Ferrari *et al*., 2010). The responses of prey to injured conspecific cues are not dependent on experience, hence allowing us to compare cross-species responses. However, different species may rely differently on chemical cues as a means to assess risk. To ensure that the four species responded similarly to risk cues before CO_2 treatment, we additionally tested the 390 ppm juveniles from each species for their responses to injured conspecific cues (risk cues) and cues from injured heterospecific, which are not recognized as risk cues (Ferrari *et al*., 2010). Behavioural observations followed well-established protocols (McCormick, 2009) and were divided into a 4-min prestimulus observation period, a 1-min cue injection period and 4-min poststimulus observation period. Reductions in feeding, in activity and in use of open microhabitats after detection of the risk cues are all common antipredator responses in prey fishes (Ferrari *et al*., 2010).

Experimental protocol. The day before testing, juveniles were placed individually in flow-through tanks (32 × 16 × 16 cm) equipped with a coral object, a sand substrate, an airstone and a 1.5 m long injection tube used to introduce stimuli into the tank, and were fed 20 mL of food (solution containing $\sim$250 *Artemia* larvae mL^{-1}). About 15 min before the start of the experiment, the flow-through system was turned off. Injured conspecific cues were prepared by making four cuts on each side of a freshly sacrificed conspecific donor fish and rinsing the donor with 15 mL of seawater. We chose this concentration of cues based on a preliminary experiment showing a gradation in behavioural responses to increasing concentrations of injured conspecific cues.

Behavioural bioassay. To stimulate activity, we injected small quantities of food into the tank, on the opposite side of the coral shelter, creating a choice for juveniles to either forage or take refuge within the coral head. The fish were fed 2.5 mL of food 5 min before the start of the trial. The trial consisted of injecting 2.5 mL of food, observing the behaviour of the fish for 4 min, injecting 15 mL of injured conspecific cues followed by 2.5 mL of food, and observing the behaviour of the fish for another 4 min. All observations were conducted blind with respect to the treatments. During each observation period, we measured three behaviours: (1) the total number of feeding strikes displayed by the fish, regardless of whether they were successful at capturing a food item or not; (2) the total number of lines the fish crossed during the observation period, using the 4 × 4 cm grid drawn on the side of the tank. A line was counted as crossed when the entire body of the fish crossed a line. This behaviour represents a measure of the swimming activity of the fish; (3) the total number of different squares visited during the observation period. This represented the two-dimensional area of activity of the fish. Prey fishes exposed to risk typically decrease or stop feeding, decrease their swimming activity and reduce their area of activity (Chivers & Smith, 1998; McCormick & Holmes, 2006). We tested 20 fish per species per treatment (mean ± SD size: *P. chrysurus*: 1.19 ± 0.07 cm, *P. moluccensis*: 1.18 ± 0.07 cm, *P. amboinensis* 1.42 ± 0.06 cm and *P. nagasakiensis*: 1.51 ± 0.06 cm). The observer was blind to the treatment, and the order of treatment was randomized. The data from each behaviour are presented as online material. We computed a proportion change in behaviour from the prestimulus baseline ([post–pre]/pre). The three behaviours were then combined into a single score principle component analysis 1 (PC1, 70% variance explained) using a correlation-matrix principal component analysis and a 3 × 4 ANOVA tested for the effect of CO_2 (390 vs. 700 vs. 850 ppm) and species on the responses of the fish to risk cues.

To test species bias in use of chemical cues, we tested 390 ppm CO_2-treated fish for response to cues from injured conspecifics (risk cues) or cues from injured heterospecific *Apogon endekataenta* (family Apogonidae) using the same experimental approach. Skin extracts were obtained from making four cuts on each side of a freshly sacrificed donor fish, and rinsing with 15 mL of seawater ($n = 20$ fish per species per treatment). Similarly to the previous experiment, a 2 × 4 ANOVA performed on the scores from the first PC1 (75% variance explained) tested for the effect of test cues (heterospecific vs. conspecific cues) and species on the responses of the juveniles.

Field assessment of behaviour and mortality

Damselfishes are susceptible to a number of predators, including moonwrasse *Thalassoma lunare*, dottyback *Pseudochromis fuscus* and lizardfishes *Synodus variegatus* and *Synodus dermatogenys* (Holmes & McCormick, 2009). These species can be seen striking at and occasionally capturing recently settled juvenile reef fishes. To compare behaviour and mortality rates among newly settled *P. chrysurus*, fish that had been exposed to each of the CO_2 treatments (390, 700 and 850 ppm) were placed singly on small patch reefs between 10:00 and 11:00 hours. Their behaviour was recorded and their survival monitored at 16:00 hours the same day, and then at 12:00 and 16:00 hours the following day.

Experimental protocol. After CO_2 treatment, *P. chrysurus* were measured (standard length: 1.19 ± 0.07 cm) and marked with a small coloured elastomer tag injected under the skin. A single individual was released onto a small reef (18 × 12 × 12 cm) made from live and dead *Pocillopora damicornis*, a common bushy hard coral. Reefs were cleared of any other fishes or invertebrates before release using a hand net. A wire cage (30 × 30 × 30 cm, 12 mm mesh size) was placed over the reef for 30 min to allow fish to acclimate to their new surroundings while being protected from predators. The 2-day survival of fish put on the reef with the cage was 100% ($n = 20$–23 for each CO_2 treatment), indicating that any mortality observed after cages were removed would be due to predation. Behaviour and mortality were recorded *in situ*. Behaviour of the 390- and 850 ppm fish were assessed over a 3-min period shortly after the cage was removed. Six aspects of behaviour were estimated using a well-established protocol: feeding rate (number of feeding strikes min^{-1}); total distance moved (cm) during the observation period; mean distance ventured (cm) from the reef; maximum distance ventured (cm); height above substratum (categorized as % of the time spent within the bottom, middle or top third of the patch) and boldness (recorded on a scale from 0 to 3, where 0 is hiding in hole and seldom emerging; 1 is retreating to hole when scared and taking >5 s to re-emerge, weakly or tentatively striking at food; 2 is shying to shelter of reef when scared but quickly emerging, purposeful striking at food; and 3, readily venturing away from reef, exploring with no hiding and striking aggressively at food). The observers were blind to the treatment, and the order the fish were set on the reefs was randomized ($n = 29$–43 fish per treatment).

The effect of CO_2 treatment (390 vs. 700 vs. 850 ppm) on the proportion of *P. chrysurus* surviving the first 30 h of settlement was analysed using two *G*-tests, comparing (1) the survival of control vs. CO_2-treated fish, and (2) the survival of 700 vs. 850 ppm fish. The behaviours were combined into a single score (PC1, 68% variance explained) using a correlation-matrix principal component analysis. The effect of CO_2 (390 vs. 850 ppm) on the behaviour of the juvenile *in situ* were analysed using a one-way ANOVA, whereby PC1 scores were used as the response variable and CO_2 treatment as a fixed factor. The data followed parametric assumptions.

Results

In the laboratory, the intensity of response to risk cues was dependent on both the CO_2 level and the species ($CO_2 \times$ species interaction: $F_{6,180} = 3.0$, $P = 0.012$, $N = 20$ per treatment, Fig. 1). All four species showed similar antipredator responses when held at 390 ppm (Fig. 1, $F_{3,60} = 2.3$, $P = 0.1$), but CO_2 reduced the antipredator responses of fish to risk, although the level of change markedly differed among species. At 700 ppm, *P. nagasakiensis* were the least affected and *P. amboinensis* the most affected ($P < 0.001$), with *P. moluccensis* and *P. chrysurus* showing intermediate patterns. At 850 ppm, *P. amboinensis*, *P. moluccensis* and *P. chrysurus* all showed similar significant losses of antipredator behaviour (Tukey *post hoc* pairwise tests: all $P > 0.7$), while *P. nagasakiensis* remained less affected (all $P < 0.001$). For all species, we observed an increased variance in the responses to cues for fish in the 700 ppm treatment (cross-species SD = 0.93), compared with control (SD = 0.43) or 850 ppm fish (SD = 0.69, Fig. 1). We reported SD, because coefficients of variation are sensitive to means nearing zero.

The cross species comparison of control fish indicated that the four species responded similarly to risk and nonrisk cues. The two-way ANOVA revealed no effect of species ($F_{3,120} = 0.7$, $P > 0.5$), a significant effect of cue ($F_{1,120} = 304$, $P < 0.001$), but no interaction between the two factors ($F_{3,120} = 1.7$, $P > 0.1$, Fig. 2) on the antipredator responses of juvenile fish. All fish displayed antipredator responses to odours from injured conspecifics, but did not alter their behaviour in responses to cues from injured distantly related apogonids.

In the field, CO_2-treated *P. chrysurus* were more active, moved further and higher away from the reef, displayed higher feeding rates and were bolder than control fish (ANOVA: control vs. 850 ppm: $F_{1,54} = 15.4$, $P < 0.001$). CO_2-treated *P. chrysurus* also suffered much higher mortality during the first 30 h of settlement

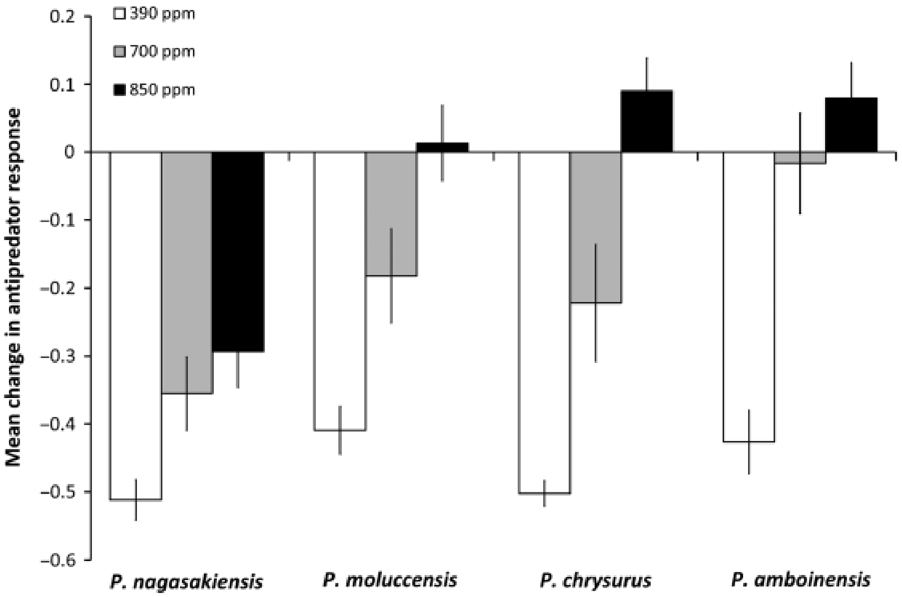

Fig. 1 Mean (± SE) proportion change from the prestimulus baseline in three antipredator behaviours (averaged) displayed in response to a risk cue (injured conspecific cues). Negative numbers represent an adaptive antipredator response ($N = 20$ treatment^{-1}).

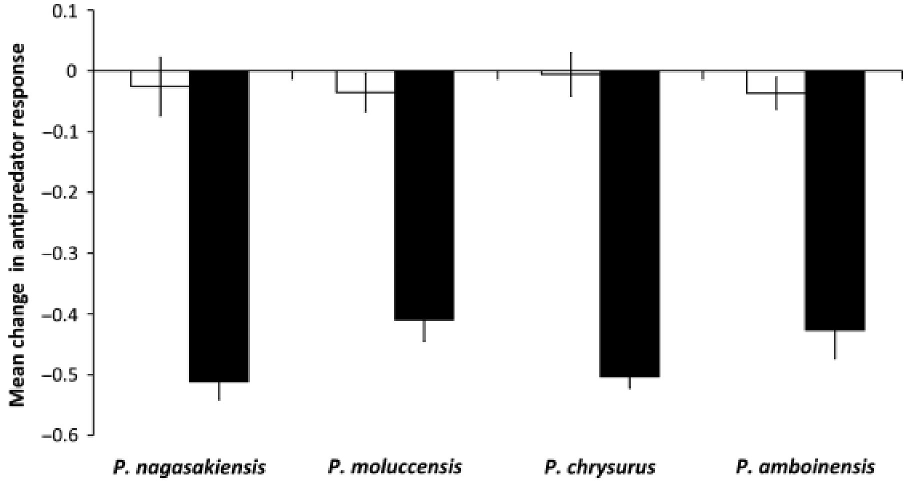

Fig. 2 Mean (± SE) proportion change from the prestimulus baseline in three antipredator behaviours (averaged) displayed in response to a nonrisk cue (Apogonid skin extract – empty bars) or to a risk cue (conspecific skin extract – solid bars). Negative numbers represent an adaptive antipredator response ($N = 20$ per treatment).

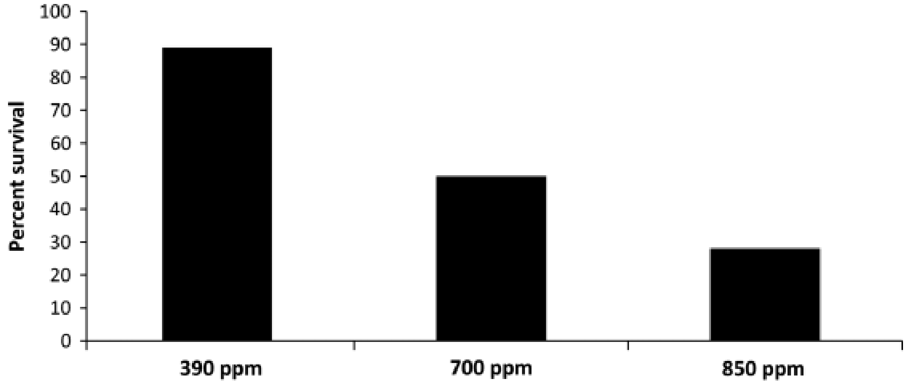

Fig. 3 Percent of *Pomacentrus chrysurus* surviving during the first 30 h of settlement on a coral reef, following exposure to different CO_2 levels ($N = 29$–43 per treatment).

(Fig. 3, G-tests: $N = 29$–43 per treatment; control vs. elevated CO_2: $G = 19.8$, $P < 0.005$; 700 vs. 850 ppm: $G = 3.4$, $P = 0.07$).

Discussion

When inspected in the laboratory, CO_2-exposed fish clearly lack the adaptive antipredator responses to risk cues exhibited by control fish. As CO_2 increased, individuals decreased the intensity of their antipredator response towards the risk cues. This is consistent with previous laboratory studies, showing reductions in both olfactory predator detection (Dixson *et al.*, 2010) and homing behaviour (Munday *et al.*, 2009a). In addition, we observed an increased variation in the responses of fish to risk in the 700 ppm treatment, compared with the control and 850 ppm treatments. A greater variability in the effect of CO_2 indicates that some individuals are much more affected than others under these conditions, and thus, 700 ppm might represent a threshold for which biological adaption may be possible. These observations are consistent with previous work (Munday *et al.*, 2010) reporting greater variability in the effect of CO_2 at that level. They showed that, when presented in a flume containing the odour of a predator in one arm and control water in the other, roughly half of the juvenile damselfish, *Pomacentrus wardi*, treated with 700 ppm CO_2 preferred the water side (nonaffected) while the other half preferred the predator side (affected). Given that up to 60% of new recruits can be consumed by predators in a single night (Caley *et al.*, 1996), even a slight difference in survival could lead to considerable opportunity for selection of those CO_2 tolerant phenotypes.

In addition to the marked intraspecific variation, our results indicate striking variation in the magnitude of CO_2 effects among four congeneric species.

P. amboinensis appear as a very sensitive species, showing a ~95% reduction in antipredator response at levels as low as 700 ppm, which suggests that they would likely show a maladaptive response at CO_2 levels even lower than those tested here. In contrast, *P. nagasakiensis* was less affected – *only* showing 30% and 40% reduction in antipredator response at 700 and 850 ppm – and consequently should have the greatest opportunity to adapt and possibly even gain indirect benefits (e.g., via decreased competition) as CO_2 levels rise over the next decades. These effects are likely unrelated to body size as *P. amboinensis* and *nagasakiensis* were the largest juveniles of the group. What can explain this variation? All species are closely related *Pomacentrus* species, found in sympatry, and showing similar life history traits (Wellington & Victor, 1989). Phylogenetic distances between our four species does not seem to correlate with our results, given that *P. moluccensis* and *P. amboinensis* are more related than *P. moluccensis* and *P. chrysurus* (Cooper *et al.*, 2009). All species share a similar life history, recruiting back to the reef at the same time and same age (Wellington & Victor, 1989), feeding on the same food, susceptible to the same predators. On the reefs, we observe difference in habitat use, which some species preferring rubbles (*P. chrysurus*, *P. nagasakiensis*), while others prefer life coral (*P. amboinensis*, *P. moluccensis*) (Ohman *et al.*, 1998). Future work should focus on the role of physiology or life history in explaining these variations. If all classes of fish show this degree of variation in their responses to CO_2, making specific predictions about changes in ecosystem processes and trophic dynamics under increasing CO_2 levels will be challenging. Nevertheless, identifying species differences in CO_2 tolerance is the first step in predicting such changes.

The CO_2-induced alterations in antipredator behaviour observed in the lab seem to have survival consequences under natural conditions. Fish with altered behavioural responses in the lab showed a fivefold (700 ppm) to sevenfold (850 ppm) increase in mortality in the wild. Although fish may survive CO_2 exposures better than other marine species (Munday *et al.*, 2009b), our results indicate that they may be as affected by ocean acidification through indirect lethal consequences of ocean acidification. Few studies have documented the fitness consequences of such alterations (Munday *et al.*, 2010).

Because we used wild caught larvae, it was not possible to treat them with CO_2 for their entire larval phase. However, previous work has established that juvenile clownfish exposed to elevated CO_2 from birth showed similar behavioural alteration as juveniles exposed for 4 days to the same levels of elevated CO_2 used here (Munday *et al.*, 2010). These results indicate that if the effects we observed were mediated by stress responses, then this stress is not solely due to the short-term nature of our CO_2 treatment and cannot be dealt with through ontogeny. Similarly, our setup did not allow us to expose successive generations of fish to CO_2 and subsequently test their ability to survive. An obvious caveat to that approach would be that captivity would alter any selection for predator avoidance, rendering survival data unrealistic. While our quantitative results may represent a 'worst case scenario' in the absence of adaptation, the qualitative data regarding interspecific variability in CO_2 tolerance provide useful information on the nature of the community changes that may unfold over the next few decades, and may also help in identifying key species to act as indicator species in the face of rising CO_2.

The transition from a pelagic to benthic existence is a critical life-history stage for many marine species and is usually associated with high levels of mortality (Caley *et al.*, 1996). Our results indicate that increased levels of CO_2 may impact recruitment patterns for coral reef fishes, and possibly other marine species. Furthermore, interspecific variation in response to rising CO_2 may result in changes to community composition of prey species, which in turn, may affect biodiversity at higher trophic levels (Walther, 2010). Both inter- and intraspecific variation will be key to the potential for adaptation of species to rising CO_2 conditions. The impact of ocean acidification on marine ecosystems will depend not only on the magnitude of species differences, but also how much and how fast these species can adapt to their novel environmental conditions, but this is currently unknown. Examining ocean acidification, alongside other environmental variables, will be a critical step in further evaluating responses to predicted climatic change.

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References

Brierley AS, Kingsford MJ (2009) Impacts of climate change on marine organisms and ecosystems. *Current Biology*, **19**, R602–R614.

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics*, **27**, 477–500.

Chivers DP, Smith RJF (1998) Chemical alarm signalling in aquatic predator–prey systems: a review and prospectus. *Ecoscience*, **5**, 338–352.

Clark D, Lamare M, Barker M (2009) Response of sea urchin pluteus larvae (Echinodermata: Echinoidea) to reduced seawater pH: a comparison among a tropical, temperate, and a polar species. *Marine Biology*, **156**, 1125–1137.

Cooper WJ, Smith LL, Westneat MW (2009) Exploring the radiation of a diverse reef fish family: phylogenetics of the damselfishes (Pomacentridae), with new classifications based on molecular analyses of all genera. *Molecular Phylogenetics and Evolution*, **52**, 1–16.

Dixson DL, Munday PL, Jones GP (2010) Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters*, **13**, 68–75.

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science*, **1**, 169–192.

Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *Ices Journal of Marine Science*, **65**, 414–432.

Ferrari MCO, Wisenden BD, Chivers DP (2010) Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. *Canadian Journal of Zoology*, **88**, 698–724.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ *et al*. (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Holmes TH, McCormick MI (2009) Influence of prey body characteristics and performance on predator selection. *Oecologia*, **159**, 401–413.

Houghton J (2004) *Global Warming: The Complete Briefing*, (3rd edn). Cambridge University Press, Cambridge.

Ishimatsu A, Hayashi M, Kikkawa T (2008) Fishes in high-CO_2, acidified oceans. *Marine Ecology-Progress Series*, **373**, 295–302.

Kleypas JA, Yates KK (2009) Coral reefs and ocean acidification. *Oceanography*, **22**, 108–117.

Kurihara H (2008) Effects of CO_2-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology-Progress Series*, **373**, 275–284.

Langer MR, Geisen M, Baumann K-H, Klas J, Riebesell U (2006) Species-specific responses of calcifying algae to changing seawater carbonate chemistry. *Geochemistry, Geophysics and Geosystematics*, **7**, Q09006, doi: 10.1029/2005GC001227.

Luthi D, Le Floch M, Bereiter B *et al*. (2008) High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature*, **453**, 379–382.

McCormick MI (2009) Behaviourally mediated phenotypic selection in a disturbed coral reef environment. *Plos One*, **4**.

McCormick MI, Holmes TH (2006) Prey experience of predation influences mortality rates at settlement in a coral reef fish, *Pomacentrus amboinensis*. *Journal of Fish Biology*, **68**, 969–974.

Meehl GA, Stocker TF, Collins P *et al*. (2007) Global climate projection. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report on the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M *et al*.), pp. 747–845. Cambridge Press, Cambridge.

Meekan MG, Milicich MJ, Doherty PJ (1993) Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. *Marine Ecology-Progress Series*, **93**, 217–225.

Meekan MG, Wilson SG, Halford A, Retzel A (2001) A comparison of catches of fishes and invertebrates by two light trap designs, in tropical NW Australia. *Marine Biology*, **139**, 373–381.

Melzner F, Gutowska MA, Langenbuch M *et al*. (2009) Physiological basis for high CO_2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences*, **6**, 2313–2331.

Miller AW, Reynolds AC, Sobrino C, Riedel GF (2009) Shellfish face uncertain future in high CO_2 world: influence of acidification on oyster larvae calcification and growth in estuaries. *Plos One*, **4**.

Munday PL, Dixson DL, Donelson JM, Jones GP, Pratchett MS, Devitsina GV, Doving KB (2009a) Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 1848–1852.

Munday PL, Dixson DL, McCormick MI, Meekan M, Ferrari MCO, Chivers DP (2010) Replenishment of fish populations is threatened by ocean acidification. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 12930–12934.

Munday PL, Donelson JM, Dixson DL, Endo GGK (2009b) Effects of ocean acidification on the early life history of a tropical marine fish. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 3275–3283.

Ohman MC, Munday PL, Jones GP, Caley MJ (1998) Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology*, **225**, 219–238.

Orr JC, Fabry VJ, Aumont O *et al*. (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681–686.

Parker LM, Ross PM, O'Connor WA (2010) Comparing the effect of elevated pCO(2) and temperature on the fertilization and early development of two species of oysters. *Marine Biology*, **157**, 2435–2452.

Portner HO, Farrell AP (2008) Physiology and climate change. *Science*, **322**, 690–692.

Portner HO, Langenbuch M, Michaelidis B (2005) Synergistic effects of temperature extremes, hypoxia, and increases in CO_2 on marine animals: from earth history to global change. *Journal of Geophysical Research-Oceans*, **110**, C09S10, doi: 10.1029/2004JC002561.

Portner HO, Langenbuch M, Reipschlager A (2004) Biological impact of elevated ocean CO_2 concentrations: lessons from animal physiology and earth history. *Journal of Oceanography*, **60**, 705–718.

Raupach MR, Marland G, Ciais P, Le Quere C, Canadell JG, Klepper G, Field CB (2007) Global and regional drivers of accelerating CO_2 emissions. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 10288–10293.

Ries JB, Cohen AL, McCorkle DC (2009) Marine biocalcifiers exhibit mixed responses to CO_2-induced ocean acidification. *Geology*, **37**, 1131–1135.

Rosa R, Seibel BA (2008) Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 20776–20780.

The Royal Society (2005) *Ocean Acidification Due to Increasing Atmospheric Carbon Dioxide*. The Royal Society, London.

Walther GR (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**, 2019–2024.

Wellington GM, Victor BC (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Marine Biology*, **101**, 557–567.

Widdicombe S, Spicer JI (2008) Predicting the impact of ocean acidification on benthic biodiversity: what can animal physiology tell us? *Journal of Experimental Marine Biology and Ecology*, **366**, 187–197.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Mean proportion change in (a) feeding strikes, (b) line crosses and (c) area ue for *Pomacentrus moluccensis*, *amboinensis*, *nagazakiensis* and *chrysurus*, exposed to 390 (control), 700 or 850 ppm CO_2.