Ocean acidification reverses competition for space as habitats degrade

Mark I. McCormick, Sue-Ann Watson & Philip L. Munday

ARC Centre of Excellence for Coral Reef Studies and School of Marine and Tropical Biology, James Cook University, Townsville, Queensland, Australia.

How marine communities are affected by CO2-induced climate change depends on the ability of species to tolerate or adapt to the new conditions, and how the altered characteristics of species influence the outcomes of key processes, such as competition and predation. Our study examines how near future CO2 levels may affect the interactions between two damselfish species known to compete for space, and the effects of declining habitat quality on these interactions. The two focal species differed in their tolerance to elevated CO2, with the species that is competitively dominant under present day conditions being most affected. Field experiments showed that elevated CO2 (945 μatm) reversed the competitive outcome between the two species with mortal consequences, and this reversal was accentuated in degraded habitats. Understanding these complex interactions will be crucial to predicting the likely composition of future communities under ocean acidification and climate change.

The impact of climate change on marine communities will depend on how species' differences in physiological tolerances and performance alter biological interactions within a changing resource landscape1–3. Rising atmospheric CO2 over the last century has already led to a reduction in ocean pH (ocean acidification) and an increase in ocean temperature4. Dissolved CO2 levels in the ocean are rising in line with atmospheric CO25 and are projected to exceed 900 μatm from the current day 390 μatm by 21006, while temperatures of the coastal ocean may increase by up to 3 °C4. Coral reefs are particularly susceptible to these changes as they have evolved under relatively stable environmental conditions and many organisms may live near their maximum physiological tolerance limits for temperature and CO27,8. How reef communities are affected will be dependent on the ability of species to tolerate or adapt to the new conditions and how the altered characteristics of species influence the outcomes of key processes, such as competition and predation9.

Elevated levels of CO2 affect the acid-base balance of marine organisms10 and alters the processing of sensory information for organisms as diverse as snails, crabs and fishes11–13. For fishes this effect occurs through modification to the functioning of neuropeptidergic5, which changes the way individuals interact with their habitats and with predators, leading to increased levels of mortality, particularly at critical life history bottlenecks such as settlement5,10. While research demonstrates major changes in behaviour and performance for isolated individuals, it is unknown how these conditions are likely to influence the biological interactions that form the foundation of community dynamics.

Ocean acidification and elevated temperature also affect the live coral that is an important source of shelter and food for many coral reef fishes. High CO2 leads to a reduction in seawater pH that decreases the availability of carbonate ions required for coral skeleton growth9. In addition, ocean warming causes corals to lose the symbiotic zooxanthellae that produce much of their required food14. This coral bleaching has been responsible for wide scale loss of coral, and combined with the effect of storms has resulted in widespread degradation of live coral and the fish communities that associate with them15–21. While shifts in fish community composition have been associated with coral degradation, it is unclear how degraded reef habitat will affect interactions among fishes that live in these environments in a high CO2 world.

Marine fishes display inter- and intra-specific variability in the extent to which they are affected by CO2-driven modifications to their environment. While many species require live bushy coral as a nursery habitat15,22, many have the flexibility to satisfy their resource requirements from a broader resource base and are not confined to one habitat (often classed as habitat generalists). Moreover, some fish species are more susceptible than others to the effects of elevated CO216,23, and even within species there can be high variability in the degree to which sensory systems are compromised13. This variability in the way species are affected modifies the selection profiles by predators on juvenile fishes under moderately elevated CO2 (~800–900 μatm CO2)24–26. One of the fundamental processes that affect the susceptibility of individuals to predation is how the prey within a multispecies assemblage...
interact to modify individual risk. Interference competition, is particularly important in affecting the small scale distribution of growth, body size, body condition and distribution in relation to predation risk. While there are some studies demonstrating differences in sensitivity to CO2 among damselfish species, it is unclear how these differences may affect behavioural interactions under natural conditions of predation risk.

These effects will not occur in isolation, but rather as the coral habitats degrade fishes that inhabit these habitats will themselves be battling to adapt physiologically to the new resources and balance of senses available to them for risk assessment. Our study examined how CO2 levels projected to occur in the next 70–100 y may affect the interactions between two damselfish species known to compete for space at settlement and how these interactions were modified in coral habitat degraded through bleaching. First, we reared wild-caught damselfish larvae of the two species (Pomacentrus amboinensis and P. moluccensis) in elevated CO2 (945 µatm) or control water for 4 days, which we have previously shown to be sufficiently long to yield the lasting behavioural effects associated with CO2-induced neuroreceptor modification. Secondly, we transplanted treated fish to an array of natural reefs made of unbleached or bleached hard coral in a 2 × 2 design to test if exposure to elevated CO2 and coral state interacted to alter the behaviour of fishes and their risk of mortality during recruitment to adult habitat. Because CO2 impairs the senses used to detect and respond to habitat characteristics and assess predation, we predicted that the effects of CO2 might interact with habitat state to affect behaviour and ultimately survival. Our results show that elevated CO2 reverses the competitive outcome between the two species with mortal consequences and that this reversal is accentuated in degraded habitats.

### Results

There was a significant difference in mortality of P. moluccensis among the four treatments ($X^2 = 20.05$, df = 3, $p = 0.0002$). Fish from elevated CO2 on unbleached coral had approximately four times the survival of fish from the other three treatments (Fig. 1a), indicating that there was an interaction between CO2 treatment and coral state. Mortality curves for P. amboinensis also differed from one another ($X^2 = 36.7728$, df = 3, $p < 0.0001$), with fish that had been exposed to elevated CO2 having lower survival than those from current day CO2 conditions (Fig. 1b). Those exposed to elevated CO2 on bleached coral died within 48 h, while over 50% of fish from present day CO2 conditions survived 72 h (Fig. 1b).

The maximum distance fishes ventured away from the coral shelter was affected by coral state and differed between species, but this species-specific effect was largely reversed with elevated CO2 (Species × State × CO2 treatment: $F_{1,208} = 5.10$, $p = 0.025$; Fig. 2a). On unbleached coral at ambient CO2, both species stayed a similar distance from the coral. However, on bleached coral, P. moluccensis was over twice as far from shelter than P. amboinensis. The trends between species were largely reversed by elevated CO2 conditions (Fig. 2b). On healthy coral P. moluccensis stayed closer to the coral, at a distance that did not differ from ambient CO2 condition. In contrast, P. amboinensis was located almost 4 times as far from unbleached coral than when exposed to ambient CO2 conditions, and twice as far from the unbleached coral than P. moluccensis. These trends were accentuated when the patch reef comprised of bleached coral (Fig. 2b). The height of fish on patch reefs differed between species, but the magnitude of the effect changed with CO2 conditions experienced (Species × CO2 treatment: $F_{1,208} = 12.31$, $p < 0.0006$). P. amboinensis occupied the lower part of the patch regardless of CO2 treatment or coral state, while P. moluccensis occupied the highest part of the reef, but was significantly closer to the bottom when fish had been exposed to elevated CO2 (Tukey’s test, $p < 0.05$; Fig. 3).

The levels of aggression exhibited by fish to their size-matched pair was strongly affected by coral state and differed between species, but this species-specific effect was reversed with elevated CO2 (Species × State × CO2 treatment: $F_{1,208} = 11.757$, $p = 0.0007$; Fig. 4). Under ambient CO2 conditions, P. amboinensis was much more aggressive than P. moluccensis with the dominant P. amboinensis being more aggressive on bleached coral (Fig. 4a). In contrast, under elevated CO2 conditions the pattern was reversed by species, with P. moluccensis being most aggressive on bleached coral compared to unbleached coral, but always more aggressive than P. amboinensis (Fig. 4b).

### Discussion

Elevated CO2 affected the outcome of competitive interactions between species, with a complete reversal in the species that was the most aggressive and dominant competitor. This reversal in the outcome of interference competition was most dramatic on degraded, bleached coral. The mechanism underlying this change was the differential effect of CO2 on the behaviour of the two species. A previous laboratory study has shown that P. moluccensis is less susceptible to exposure to elevated CO2 conditions than its congener P. amboinensis, who is the competitive dominant under present day conditions. For fish exposed to either current day or future CO2 conditions, the competitive interactions indirectly had mortal consequences because the aggressive interactions pushed the subordinate into areas of higher risk away from shelter; a pattern accentuated on degraded coral. The behavioural changes found in our study suggest that elevated CO2 may result in changes in the way species interact with each other and this will alter the processes that shape communities and ecosystems.

Understanding how altered species interactions affect communities and ecosystems is fundamental to predicting the impacts of climate change and ocean acidification. Previous studies on benthic communities have observed enhanced competitive dominance of algae over corals under elevated CO2. In contrast, our results show a reversal of competitive dominance, indicating that ocean acidification may lead to far more complex outcomes than would be predicted with just enhanced competitive effects. Competitive reversals between species should be commonplace under natural circumstances for organisms with strong competitive asymmetry to coexist, however they are seldom conclusively demonstrated. Steneck et al. (1991) found that depth determined which of two species of crustose coralline algae was competitively dominant, but dominance was reversed when grazing limpets reduce fitness of one species.

Under present day CO2 conditions, McCormick and Weaver (2012) found that who won the contest between P. amboinensis and P. moluccensis was strongly asymmetrical and dependent on size, over-and-above other ecological factors such as prior residency. The importance of size in dictating the outcome of competitive contests is a common finding for many organisms. P. moluccensis juveniles only started to win contests when they were 1.2 mm larger than P. amboinensis. Because the winner of competitive interactions is based on body size, the stochasticity of recruitment at small spatial scales and its pulsed nature within a tropical recruitment season will mean that neither species will always win or lose. This may lead to a destabilizing influence on the competitive dominance of any one species, making competitive exclusion less likely.

It holds therefore that changes in the competitive outcome will also occur when the species change in their ability to defend a limited resource. Studies that have examined the effect of CO2 on the behaviour of solitary damselfish juveniles demonstrate that they display a willingness to take more risk, they fail to learn predators, and as a result die faster than control fish. However, the ability to cope with elevated CO2 varies among closely related species. Ferrari et al. (2011a) exposed 5 different species of damselfish from the genus Pomacentrus to damage-release chemical alarm cues...
Fish held at current day CO$_2$ levels all responded with a fright response to the alarm cues, while those acclimated to higher CO$_2$ levels exhibited different species-specific responses from no response to the alarm cues, through to a fright response that was little different from the controls. Further, in a mesocosm study, Ferrari et al. (2011b) found that the relative mortality through predation of 5 species of damselfishes changed when both predator and prey had been exposed to elevated CO$_2$. However, the lack of behavioural information meant that the mechanism underlying the result was unclear. Our study shows that *P. amboinensis* exposed to elevated CO$_2$ also becomes less aggressive and avoids similar sized competitors that they would normally have dominated. This lowering of aggression, which underlies interference competition, is critically important for the fish to maintain its status in the plankton feeding community and will have repercussions for such ecologically important activities as obtaining food of the highest possible quality and the acquisition and defence of spawning sites.

Species are likely to acclimate to some extent to the modified chemical conditions found in future CO$_2$ conditions. However, previous studies have shown that the behavioural responses of juvenile damselfish are the same in individuals kept for 4 days at elevated CO$_2$ and those reared from hatching at the same CO$_2$ levels. Therefore, there seems to be limited prospects for within-generation acclimation of behavioural changes caused by exposure to high CO$_2$, at least during the critical early life history stages investigated here. In one of the only transgenerational studies to date, Miller et al. (2012) found that the routine metabolic rate, growth and survival of F1 offspring of the clownfish, *Amphiprion melanopus*, exposed to 1032 µatm returned to levels found in control fish as a result of non-genetic parental effects. The generality of this result is unknown but likely to vary among species. Interestingly, a recent study has demonstrated that damselfish may have limited ability to compensate for CO$_2$-induced behavioural changes through parental effects over one generation. The ability of the species used in the current study to acclimate over multiple generations by non-genetic parental effects is currently unknown, however, it is likely that competing species who have been differentially affected by CO$_2$ will be a realistic situation in the future.

CO$_2$ appears to affect early life history traits such as respiration and growth in a different way to behaviour. Currently it is unknown for any species whether behaviour is likely to adapt over generations.
to elevated CO₂. Recent studies of marine fishes and invertebrates have shown that at least part of the behavioural effect of elevated CO₂ appears to occur through a change in the gradient of acid-base relevant ions across the neuron membrane. This leads to a change in the operation of neuroreceptors (GABA-A receptors), switching them from an inhibitory to excitatory role. Research is required to determine whether this neural mechanism can adapt over multiple generations before the full ramifications of the present study can be determined.

Behavioural effects of high CO₂ will not occur in isolation; ocean warming that affects the health of corals that fish use as shelter also has direct effects on the performance of interacting fish species. A number of recent studies have found that juvenile fish that use live coral as a nursery habitat move further away from the shelter when the coral is bleached, and this exposes them to higher predation pressure in the laboratory and field. The movement away from bleached corals was also found in the current study, with the sub-ordinate species being furthest away from shelter. This was in part driven by an increase in the aggression by the dominant species, the identity of which changed in response to elevated CO₂. Ocean warming may be expected to accentuate this effect by elevating routine metabolic rates, increasing activity, and the daily food requirements, though some of this effect may be reduced through developmental and parental acclimation.

Our results represent a first step towards an understanding of how community processes may change in response to elevated CO₂. Future studies will also need to incorporate CO₂ effects on predators, who themselves could be variably affected. As demonstrated in the present study, competition can affect survival by altering an individual’s exposure to predators, either directly through aggression pushing subordinates into riskier habitats, or indirectly by elevating hunger in subordinates and in so doing influencing their balance between foraging and vigilance. Because both intra- and inter-specific competition is critically important in influencing prey vulnerability to predators investigation of the three-way interaction between dominant, subordinate and predator under elevated CO₂ will be the next crucial step in understanding the regulation of communities in a high CO₂ ocean.

**Methods**

Newly settled ambon damselfish, *Pomacentrus amboinensis* (*Pomacentridae*), and lemon damselfish, *P. moluccensis*, compete for shelter in the same live coral living space when they first settle from the plankton. Both are planktivores and show similar preferences for live, healthy coral at settlement. Interaction with the other species at the reef edge reduces the growth of both species compared to locations where the other species is absent. Within 2 mo on shallow reefs the two species display a disjunct distribution patterns with *P. amboinensis* associated with the base of the reef and *P. moluccensis* with live coral at the top of the reef.

Settlement-stage larvae of *P. amboinensis* and *P. moluccensis* were collected overnight using light traps (for design see Meekan et al. 2001) moored in open water around Lizard Island (14°40′ S, 145°28′ E), in the northern Great Barrier Reef, Australia. Fish were sorted to species and transferred to 35 L aquaria supplied with a continuous flow of either control (present day CO₂; 410 ppm; see Supplementary file) or elevated-CO₂ seawater (945 ppm; see Supplementary file) for 4 days. This period of time has been found to be sufficient to elicit the full extent of behavioural effects of high CO₂. Fish were fed 4 times daily *ad libitum* with newly hatched Artemia sp.

On the day of the field trial, fishes from the control and elevated-CO₂ treatments were placed into individually labelled plastic bags of seawater and measured with digital callipers. For each CO₂ treatment, interspecific pairs of *P. amboinensis* and
P. moluccensis were created such that the size difference between fishes was no more than 0.3 mm SL. Fish length was standardised as it has been found to be important in determining the outcome of interaction between newly settled fishes and their survivors\(^{24,28}\). There was no significant difference in size of the fish between species used in the experiment (mean ± se: P. ambionensis 11.4 ± 0.03; P. moluccensis 11.5 ± 0.03; F\(_{1,214} = 3.3, \ p = 0.07\). To reduce transport and handling stress, fish in bags were transported to the field site in a 60 L holding tank of seawater (to reduce temperature fluctuations) under subdued light conditions.

Patch reefs used in the field experiment were composed of one of two states of the bushy hard coral, *Pocillopora damicornis*: live unbleached or bleached coral. Bleached coral was produced by collecting healthy coral and placing it in freshwater for 4 minutes\(^{26}\). Over the next 48 h stressed coral lost their zooanthellae and became pale in colouration but still had their tissue intact. An array of patch reefs (~18 × 15 × 18 cm) was constructed on a sandflat, arranged 4–5 m apart and 3–6 m away from continuous reef.

Both damselfish species naturally settle on patch reefs near continuous reef. In this habitat juveniles are exposed to a diverse range of predators that use a variety of feeding modes from ambush (lizardfish *Syringedermatogyra* and small cods *Cephalopholis microprion*) to pursuit (dottybacks *Pseudochromis fuscus* and wrasse *Thalassoma lunare*). These fishes can be observed preying on juveniles that venture too far from shelter.

**Experimental protocol.** Length-matched pairs of *P. ambionensis* and *P. moluccensis* were placed onto unbleached or bleached coral patches. Patches were cleared of any other fishes or invertebrates using a hand net prior to release. Experimental fishes were released on natural reefs away from the study area. A small wire cage (~30 × 30 × 30 cm, 12 mm mesh size) was placed over the patch to allow fish to acclimatise to their new surroundings while being protected from predators. Cages were removed 40 to 60 min after release of the fish between 10:00 and 12:00 h. Fish presence was monitored 45 to 60 min after placement on the reef following the protocol of extensions from 1765 to 2300.

**Behavioural assessment.** The behaviour of each fish placed on the patch reefs was monitored 45 to 60 min after placement on the reef following the protocol of McCormick (2009)\(^{32}\). Briefly, behaviour of the focal fish was assessed over a 3 min period by a scuba diver positioned 1.0 m away from the patch with the aid of a magnifying glass. Six aspects of activity and behaviour were assessed: a) maximum distance ventured from the habitat patch; b) height above substratum (categorized as % of the time spent within the bottom, middle or upper third of the patch); c) number of fin displays; d) number of chases or bites; e) number of avoidance episodes in response to a conspecific approach. Two additional composite variables were created to summarize several of the variables recorded and enhance ecological interpretation. Relative height on the patch was summarized as a cumulative proportion of the time spent at varying heights over the 3 min observation period, with the top of the patch taken as height of 1, mid-patch a height of 0.5, and bottom a height of 0. For instance, when a fish spends 50% of its time at the top of the patch, 20% at the middle and 30% at the base the relative height value would be: (1 × 0.5) + (0.5 × 0.2) + (0 × 0.3) = 0.6. An aggression index was also created by adding the number of displays to the product of three times the number of chases and then subtracting the number of avoidance events\(^{28,42}\). Our other studies have shown that a 3 min observation period is sufficient to quantify behaviour because it is consistent in the short term (10 min to 5 days\(^{26}\)). The variable measured had been previously shown to be sensitive to competitive interactions between these two fish species\(^{41,45}\).

**Statistical analyses.** Survival (up to 72 h) of fish among the CO\(_2\) treatment (ambient and elevated) by habitat (unbleached, bleached) combinations were compared using multiple-sample Survival Analysis, which uses a Cox’s proportional hazard model (Statistica 12.0\(^{46}\)). This regression model is not based on any assumptions concerning the nature or shape of the underlying survival distribution. Survival curves of each CO\(_2\) treatment and coral state were calculated and plotted using the Kaplan–Meier product-limit method. The Kaplan–Meier method is a non-parametric estimator of survival that incorporates incomplete (censored) observations, such as those cases where censuses had to be terminated on trials prior to their completion due to time limitations of a field trip.

Three behavioural variables, maximum distance ventured, relative height and the aggression index, were compared between species, coral habitat and CO\(_2\) treatment combinations with three-factor ANOVA (Type III SS) followed by Tukey’s HSD tests. Residual analysis was used to examine assumptions of ANOVA.

1. Harley, C. D. G. Climate change, keystone predation, and biodiversity loss. *Science* **334**, 1124–1127 (2011).
2. Russell, B. D. *et al.* Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. *Biol. Lett.* **8**, 164–166 (2012).
3. Kroeker, K. J., Micheli, F. & Gambi, M. C. Ocean acidification causes ecosystem shifts via altered competitive interactions. *Nature Climate Change* **3**, 156–159 (2013).
4. Meibl, G. A. *et al.* Climate Change 2007: the physical science basis. *Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Avertit, K. B., Tignor, M., Miller, H. L. (eds) 747–846 (Cambridge, U. K., Cambridge University Press, 2007).
5. Doney, S. C. The growing human footprint on coastal and open-ocean biogeochemistry. *Science* **328**, 1512–1516 (2010).
6. Meinshausen, M. *et al.* The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change* **109**, 213–241 (2011).
7. Hoegh-Guldberg, O. *et al.* Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742 (2007).
8. Pörtner, H. O. & Farrell, A. P. Physiology and climate change. *Science* **322**, 690–692 (2008).
9. Diaz-Pulido, G., Gouzano, M., Tilbrook, B., Dove, S. & Anthony, K. R. N. High CO\(_2\) enhances the competitive strength of seaweeds over corals. *Ecol. Lett.* **14**, 156–162 (2011).
10. Pörtner, H. O., Mark, F. C. & Bock, C. Oxygen limited thermal tolerance in fish? Answers obtained by nuclear magnetic resonance techniques. *Resp. Physiol. Neurobiol.* **141**, 243–260 (2004).
37. Ferrari, M. C. O.  
36. Milicich, M. J. & Doherty, P. J.  
Larval supply of coral reef fish populations: what hope for the future?  
*J. Exp. Biol.* **215**, 3863–873 (2012).  

34. Schoener, T. W.  
Field experiments on interspecific competition.  
*Mar. Ecol. Prog. Ser.* **17**, 2980–2986 (2011a).  

33. Steneck, R. S., Hacker, S. D. & Dethier, M. N.  
Mechanisms of competitive reversal.  
*Proc. Natl. Acad. Sci. U. S. A.* **110**, 11044–11049 (2013).  

32. Dixson, D. L., Munday, P. L. & Jones, G. P.  
Ocean acidification disrupts the innate antipredator responses of fish.  
*Proc. R. Soc. Lond. b* **277**, 771–77 (2009).  

31. Doney, S. C.  
Species-specific effects of near-future CO2 on the respiratory performance of two tropical prey fish and their predator.  
*Comp. Biochem. Physiol.* **166**, 482–489 (2013).  

30. Lo¨nnstedt, O. M., McCormick, M. I. & Chivers, D. P.  
Degraded coral disrupts dominance between crustose coralline algae - an herbivore-mediated competitive reversal.  
*J. Exp. Mar. Biol. Ecol.* **414**, 62–68 (2012).  

29. Crook, E. D., Cohen, A. L., Rebolledo-Vieyra, M., Hernandez, L. & Paytan, A.  
Reduced calcification and lack of acclimatization by coral colonies growing in areas of persistent natural acidification.  
*Proc. Natl. Acad. Sci. U. S. A.* **110**, 11044–11049 (2013).  

28. Nilsson, G. E.  
Near-future CO2 levels alter fish behaviour by interference with neurotransmitter function.  
*Nature Climate Change* **2**, 201–204 (2012).  

27. Holbrook, S. J. & Schmitt, R. J.  
Competition for shelter space causes density-dependent predation mortality in damselfishes.  
*J. Exp. Biol.* **215**, 201–204 (2012).  

26. Allan, B. J. M., Domenici, P., McCormick, M. I. & Munday, P. L.  
Elevated CO2 affects predator-prey interactions through altered performance.  
*PLoS ONE* **8**, e58520 (2013).  

25. Munday, P. L.  
Selection for CO2 tolerance in marine fishes.  
*Ocean. Biol. Annu. Rev.* **8**, 11–37 (2012).  

24. Ferrari, M. C. O.  
Effects of ocean acidification on learning in coral reef fishes.  
*Oceanogr. Mar. Biol. Annu. Rev.* **4**, 277–71 (2009).  

23. Steneck, R. S.  
Effects of ocean acidification on coral reef fish populations.  
*Mar. Ecol. Prog. Ser.* **17**, 2980–2986 (2011a).  

22. Ho¨lter, S. J. & Schmitt, R. J.  
Competiton for shelter space causes density-dependent predation mortality in damselfishes.  
*Ecology* **83**, 2855–2868 (2002).  

21. Doherty, P. J. & Williams, D. M.  
The replenishment of coral reef fish populations.  
*Oceanogr. Mar. Biol. Annu. Rev.* **26**, 487–551 (1988).  

20. Doherty, P. J. & Widdicombe, S.  
Larval supply of coral reef fish populations: magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef.  
*Mar. Ecol. Prog. Ser.* **110**, 121–134 (1994).  

19. Jones, G. P., McCormick, M. I., Srinivasan, M. & Eagle, J. V.  
Coral decline reverses competition for space as habitats degrade.  
*Proc. Natl. Acad. Sci. U. S. A.* **110**, 11044–11049 (2013).  

18. Nilsson, G. E.  
Near-future CO2 levels alter fish behaviour by interference with neurotransmitter function.  
*Nature Climate Change* **2**, 201–204 (2012).  

17. Crook, E. D., Cohen, A. L., Rebolledo-Vieyra, M., Hernandez, L. & Paytan, A.  
Reduced calcification and lack of acclimatization by coral colonies growing in areas of persistent natural acidification.  
*Proc. Natl. Acad. Sci. U. S. A.* **110**, 11044–11049 (2013).  

16. Ferrari, M. C. O.  
Effects of ocean acidification on learning in coral reef fishes.  
*Oceanogr. Mar. Biol. Annu. Rev.* **4**, 277–71 (2009).  

15. Munday, P. L. et al.  
Ocean acidification alters larval behaviour and impedes recruitment to reef fish populations.  
*PNAS* **107**, 12930–12934 (2010).  

14. Nilsson, G. E. et al.  
Near-future CO2 levels alter fish behaviour by interference with neurotransmitter function.  
*Nature Climate Change* **2**, 201–204 (2012).  

13. Munday, P. L., McCormick, M. I. & Nilsson, G. E.  
Impact of global warming and rising CO2 on coral reef fishes: what hope for the future?  
*J. Exp. Biol.* **215**, 3863–873 (2012).  

12. Briffa, M., de la Haye, K. L. & Munday, P. L.  
High CO2 and marine animal behaviour: Potential mechanisms and ecological consequences.  
*Mar. Poll. Bull.* **64**, 1519–1528 (2012).  

11. Watson, S.-A. et al.  
Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels.  
*Proc. R. Soc. Lond. b* (2013) doi: 10.1098/rspb.2013.2377.  

10. Ferrari, M. C. O.  
Effects of ocean acidification on learning in coral reef fishes.  
*Oceanogr. Mar. Biol. Annu. Rev.* **4**, 277–71 (2009).  

9. Jones, G. P., McCormick, M. I., Srinivasan, M. & Eagle, J. V.  
Coral decline threatens fish biodiversity in marine reserves.  
*PNAS* **101**, 8251–8253 (2004).  

8. Pratchett, M. S. et al.  
Effects of climate-induced coral bleaching on coral-reef fishes - ecological and economic consequences.  
*Oecolog. Mar. Biol. Annu. Rev.* **46**, 251–296 (2008).  

7. Osborne, K., Dolman, A. M., Burgess, S. C. & Johns, K. A.  
The dynamics of coral cover on the Great Barrier Reef (1995–2009).  
*PLoS ONE* **6**, e17516 (2011).  

6. Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H. & Pratchett, M. S.  
Recovery of an isolated coral reef system following severe disturbance.  
*Science* **340**, 69–71 (2013).  

5. Couturier, C. S., Stecky, J. A. W., Rummer, J. L., Munday, P. L. & Nilsson, G. E.  
Species-specific effects of near-future CO2 on the respiratory performance of two tropical prey fish and their predator.  
*Comp. Biochem. Physiol.* **166**, 482–489 (2013).  

4. Ferrari, M. C. O. et al.  
Putting prey and predator into the CO2 equation - quantitative and qualitative effects of ocean acidification on predator-prey interactions.  
*Ecol. Let.* **14**, 1143–1148 (2011b).  

3. Munday, P. L. et al.  
Selection for CO2 tolerance in marine fishes.  
*Ocean. Biol. Annu. Rev.* **8**, 11–37 (2012).  

2. Allan, B. J. M., Domenici, P., McCormick, M. I. & Munday, P. L.  
Elevated CO2 affects predator-prey interactions through altered performance.  
*PLoS ONE* **8**, e58520 (2013).  

1. Holbrook, S. J. & Schmitt, R. J.  
Competition for shelter space causes density-dependent predation mortality in damselfishes.  
*Ecology* **83**, 2855–2868 (2002).  

**Acknowledgments**  
Logistic support was provided by staff at the Lizard Island Research Station (Australian Museum). Cecilia Villa-Cort{e}a Rath and Matthew Mitchell assisted MIM with the field component of the study. Oona L{ö}nnstedt provided useful comments on a draft of the manuscript. Funding was provided through the ARC Centre of Excellence for Coral Reef Studies (CE0561432).  

**Author contributions**  
MIM designed the study. S.-A. W. operated the CO2 dosing system. MIM undertook the fieldwork. MIM, P.L.M. and S.-A. W. wrote the paper.  

**Additional information**  
Supplementary information accompanies this paper at http://www.nature.com/scientificreports  

**Competing financial interests:** The authors declare no competing financial interests.  

**How to cite this article:** McCormick, M.I., Watson, S.-A. & Munday, P.L. Ocean acidification reverses competition for space as habitats degrade.  
*Sci. Rep.* **3**, 3280; DOI:10.1038/srep03280 (2013).  

This work is licensed under a Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported license. To view a copy of this license, visit http://creativecommons.org/licenses/by-nc-nd/3.0