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Author for correspondence:
Sue-Ann Watson
e-mail: sueann.watson@jcu.edu.au

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Global change biology

Ocean acidification alters predator behaviour and reduces predation rate

Sue-Ann Watson[1], Jennifer B. Fields[2] and Philip L. Munday[1]

[1]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia
[2]Pitzer College, Claremont, CA 91711, USA

S-AW, 0000-0002-9818-7429

Ocean acidification poses a range of threats to marine invertebrates; however, the emerging and likely widespread effects of rising carbon dioxide (CO_2) levels on marine invertebrate behaviour are still little understood. Here, we show that ocean acidification alters and impairs key ecological behaviours of the predatory cone snail *Conus marmoreus*. Projected near-future seawater CO_2 levels (975 µatm) increased activity in this coral reef molluscivore more than threefold (from less than 4 to more than 12 mm min^{-1}) and decreased the time spent buried to less than one-third when compared with the present-day control conditions (390 µatm). Despite increasing activity, elevated CO_2 reduced predation rate during predator–prey interactions with control-treated humpbacked conch, *Gibberulus gibberulus gibbosus*; 60% of control predators successfully captured and consumed their prey, compared with only 10% of elevated CO_2 predators. The alteration of key ecological behaviours of predatory invertebrates by near-future ocean acidification could have potentially far-reaching implications for predator–prey interactions and trophic dynamics in marine ecosystems. Combined evidence that the behaviours of both species in this predator–prey relationship are altered by elevated CO_2 suggests food web interactions and ecosystem structure will become increasingly difficult to predict as ocean acidification advances over coming decades.

1. Introduction

Rising carbon dioxide (CO_2) levels and subsequent ocean acidification affect the survival, growth, calcification and reproduction of marine organisms [1]. However, recent research shows CO_2 levels projected for the end of the century ($pCO_2 \leq 1000$ µatm, Representative Concentration Pathway, RCP 8.5 [2]) also alter marine invertebrate behaviour, including in tropical [3] and temperate [4,5] gastropod molluscs, cephalopod molluscs [6] and crustaceans [7,8]. Notably, behavioural effects are apparent even at modest CO_2 levels where effects on physiology are not yet manifest [3,9]. Furthermore, evidence that elevated CO_2 may alter behaviour by interfering with the function of $GABA_A$ neurotransmitter receptors in fishes [10] and invertebrates [3,11] suggests behavioural alteration among trophic levels for water-breathing vertebrates and invertebrates [12] is likely to be widespread. For calcifying invertebrates, the rapidly emerging, and likely global reach of behavioural alteration means they now face the dual threats of both impaired calcification and altered behaviour at projected future CO_2 levels. Invertebrates dominate lower trophic levels, exhibiting diversities at least an order of magnitude greater than vertebrates in marine ecosystems (e.g. [13]). Understanding the behavioural effects of ocean acidification on invertebrates is thus critical to determine the full impacts of anthropogenic CO_2 emissions on the oceans.

Predator–prey interactions shape the structure of marine communities and ecosystems [14]. However, we know little about the potential effects of ocean acidification on predatory behaviours in marine invertebrates, or the potential for ocean acidification to affect invertebrate behaviour across more than one trophic level. Several studies have shown that the response of invertebrate prey species to their predator is affected by high CO_2 [3–5,15,16], but how elevated CO_2 may affect the predators of these species has not been tested. For a temperate gastropod, one recent study showed that elevated CO_2 affected the avoidance of predator cues, but not cue detection of mussel prey [5]. Here, to determine the potential effects of elevated CO_2 on predator behaviour and predation rate, we assess the effects of near-future CO_2 levels (RCP 8.5 [2]) on the behaviour of the venomous marbled cone snail *Conus marmoreus* Linnaeus, 1758, a molluscivorous predator that inhabits coral reefs and is often an ambush or stealth hunter of other gastropods. Previous work has shown elevated CO_2 affects the antipredator behaviour of its prey, the humpbacked conch *Gibberulus gibberulus gibbosus* (Röding, 1798) [3], but how elevated CO_2 might affect the predator, and thus predator–prey interactions between these species, is unknown. Specifically, we investigate whether exposure to elevated CO_2 affects both general behaviour and prey-capture behaviours in this predatory invertebrate.

2. Material and methods

We exposed cone snails to control (390 µatm) and elevated (975 µatm) CO_2 conditions (table 1) for two to three weeks using established methods (e.g. [3]). General behaviours (distance travelled and speed, direction moved, left- or right-side preferences, time taken to bury, time spent buried) were tested on individuals in a large circular arena tank over 15 min. Righting was tested separately over 30 min. Initial predator–prey interactions were conducted in the circular arena over 15 min and longer predator–prey experiments over 32 h were performed in 32 l aquaria. Prey used in experiments were from control CO_2 conditions and a natural sand substrate was provided for all trials. Generalized linear models and survival analyses were used to test for the effects of CO_2 on predator behaviour and predation success, respectively. Full details of the experimental system, seawater manipulation and behavioural experiments are provided in the electronic supplementary material. Data are available from the Dryad Digital Repository [17].

3. Results

(a) General behaviour

Elevated CO_2 increased the distance travelled by cone snails during the 15 min trial ($t_{20} = 2.521$, $p = 0.020$; figure 1). At 975 µatm CO_2, cone snails moved three to four times further (186.0 ± 59.0 mm, mean ± s.e.) than at control conditions (56.1 ± 6.5 mm), equivalent to a mean movement speed of 12.4 mm min^{-1} at elevated CO_2 conditions, compared with 3.7 mm min^{-1} at control conditions (figure 1). There was no difference, however, in the direction of movement ($W_2 = 3.046$, $p = 0.218$), with a circular mean of 349.8° for control and 351.8° for elevated CO_2 cone snails. The number of left- and right-side choices was distributed equally in control predators (54.5%); however, 81.8% of elevated CO_2 predators finished the trial left of the starting line and one elevated CO_2 predator turned in a complete circle, although there was no significant difference in left-side preference ($\chi^2 = 1.932$, d.f. = 1, $p = 0.165$). In general, control predators tended to travel in a straighter line than elevated CO_2 predators, whose trajectory tended to curve.

During the 15 min trial, 81.8% of control predators buried; however, only 27.3% of elevated CO_2 predators buried. Resultantly, the amount of time spent buried was greater at control (6.0 ± 1.2 min) than at elevated CO_2 condition (1.6 ± 0.9 min) ($t_{20} = -2.362$, $p = 0.028$; figure 1). However, for the predators that chose to bury, there was no difference in time taken to bury between CO_2 treatments ($t_{10} = 0.691$, $p = 0.505$) with mean time taken to bury being 7.7 ± 0.9 min at control and 9.0 ± 1.8 min at elevated CO_2 conditions. In self-righting trials, nine cone snails righted in each treatment after 30 min. There was no significant difference in righting time with CO_2 ($t_{16} = 2.100$, $p = 0.052$; figure 1), although there was a trend for increased self-righting time at elevated CO_2 (16.4 ± 1.4 min, mean ± s.e.) compared with control (11.4 ± 1.9 min) conditions.

(b) Predator–prey interactions

Elevated CO_2 increased cone snail activity during the 15 min predator–prey interaction with elevated CO_2 cone snails moving 255.1 ± 93.6 mm (mean ± s.e.) compared with 32.1 ± 6.4 mm for control cone snails ($t_{15} = 2.541$, $p = 0.023$; figure 1). There was no significant difference, however, in the distance between the predator and the prey at the end of the trial ($t_{15} = 0.791$, $p = 0.441$; figure 1); the mean distance of elevated CO_2 predators from the prey was 370.2 ± 90.8 mm compared with 291.0 ± 41.2 mm for control predators, and no predators captured their prey during the 15 min trial, which could have influenced activity. Number of days in treatment had no effect on distance travelled ($t_{15} = -0.602$, $p = 0.556$) or distance from prey ($t_{15} = 0.022$, $p = 0.983$). During the longer 32 h predator–prey interactions, there were significant differences in the survival trajectories of prey for control and elevated CO_2 predators ($\chi^2 = 4.830$, d.f. = 1, $p = 0.028$; figure 2), with more than half (60%) of control predators successfully capturing and consuming their prey, compared with only 10% of elevated CO_2 predators.

4. Discussion

Our findings show that projected end-of-century CO_2 conditions [2] affect a range of both general and hunting behaviours of predatory invertebrates, in this case a tropical predatory mollusc. Elevated CO_2 (975 µatm) increased activity by increasing the distance travelled and thus average speed by more than 3× control levels, and reduced the amount of time spent buried to one-third of control levels. Ocean acidification can increase activity in squid [6] and in the current study increased activity and a reduction in the time spent buried may be a result of increased boldness at elevated CO_2, similar to previous findings in fishes [18]. Elevated CO_2 did not significantly affect self-righting ability in this predator, nor (as previously found) its prey [3], although elevated CO_2 can alter self-righting time in a temperate mollusc [4].

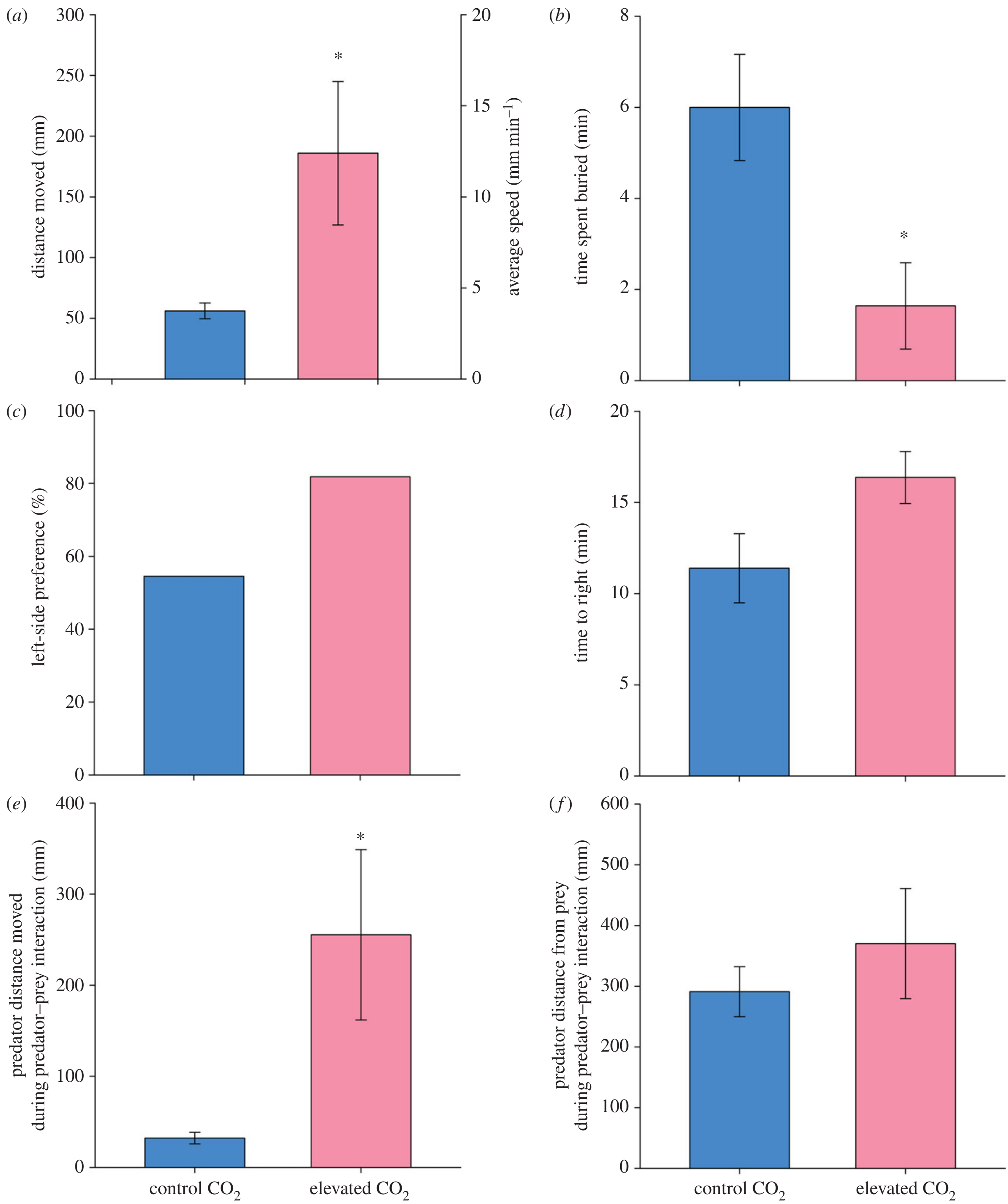

Figure 1. Effect of ocean acidification on key ecological behaviours of the predatory marbled cone snail: (*a*) distance travelled and speed, (*b*) time spent buried, (*c*) percentage of individuals that finished the trial on the left side of the test arena, (*d*) time to right; and during the 15 min predator–prey interaction in the arena: (*e*) distance travelled by the predator and (*f*) predator distance from prey. Blue and pink bars show control and elevated CO_2-treated predators, respectively. Values are means $\pm$ s.e. Asterisk (*) denotes a significant difference. (Online version in colour.)

While ocean acidification increased activity, predators had reduced foraging and prey-capture success. During predator–prey interactions, distance moved was increased (more than 3×) at elevated CO_2 levels, but although an increase in distance covered might be expected to increase foraging success, predators were no closer to their prey at the end of the 15 min trial. During the 32 h trial, prey-capture success was reduced markedly from 60 to 10%. Cone snails are often found buried in sandy areas in coral reefs, lying in ambush for their prey. Elevated CO_2 could reduce predation rate by: (i) increasing activity and consequently decreasing the time spent buried lying-in-wait for prey—potentially altering prey-capture strategy; (ii) reducing the ability to detect or capture prey (but see [5]); (iii) reducing motivation to feed; or (iv) a combination of altered decision-making behaviours. Additionally, increased activity

Table 1. Seawater carbonate chemistry for each treatment.

group	treatment	temperature (°C)	salinity	pH_{NBS}	total alkalinity (μmol kg^{-1} SW)	pCO_2 (μatm)	Ω_{Ca}	Ω_{Ar}
A	control	28.2 (±0.2)	35.5	8.19 (±0.01)	2297.9 (±3.3)	389.3 (±7.1)	5.70 (±0.08)	3.80 (±0.05)
A	elevated-CO_2	28.4 (±0.1)	35.5	7.86 (±0.00)	2288.3 (±4.3)	973.9 (±9.0)	3.04 (±0.02)	2.03 (±0.02)
B	control	27.8 (±0.3)	35.5	8.19 (±0.01)	2278.6 (±13.9)	387.1 (±8.8)	5.58 (±0.10)	3.71 (±0.07)
B	elevated-CO_2	27.8 (±0.3)	35.5	7.85 (±0.00)	2266.6 (±16.5)	975.5 (±7.4)	2.93 (±0.03)	1.95 (±0.02)

Values are means ± s.e.

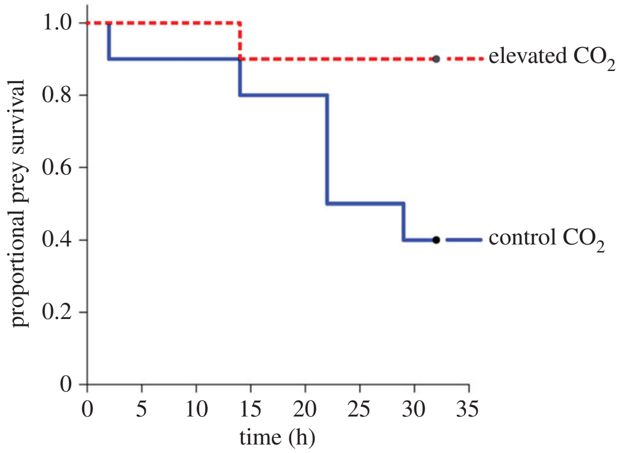

Figure 2. Effect of ocean acidification on prey-capture success. Survival trajectories of humpbacked conch prey during predator–prey interactions. Blue (solid) and red (dashed) lines show control and elevated CO_2-treated predators, respectively. (Online version in colour.)

levels are likely to result in a greater energetic demand, so reductions in prey-capture rate may have energy budget consequences for these predators. A shift in the balance of energy intake versus expenditure would have a direct effect on individual performance and could potentially impact on optimal foraging strategies [19].

Our previous research showed that elevated CO_2 levels (961 μatm) alter antipredator behaviours of the prey snail, the humpbacked conch [3], making it more vulnerable to predation. Here, we additionally find effects of elevated CO_2 on the behaviour of the predator, providing the first evidence of behavioural alteration caused by ocean acidification across two invertebrate trophic levels. Combinations of behavioural changes such as these are likely to alter trophic interactions in marine food webs, including for keystone species [4,5]. The prevalence of complex trophic interactions in marine ecosystems, often involving multiple species and indirect effects, means that behavioural alterations caused by elevated CO_2 levels are likely to make future ecosystem structure and function more difficult to predict. Increasing evidence for behavioural effects of elevated CO_2 on species at different trophic levels [3–8,12,15,16,18,20,21], including interacting species as demonstrated here, suggests that trait-mediated indirect interactions could be important in predicting the effects of ocean acidification on marine communities and deserve further attention [19].

This study tested the potential effect of ocean acidification on predator behaviour. Although it was not possible to determine the effect of elevated CO_2 on both the predator and the prey simultaneously owing to limited predator sample sizes, future research should examine how predator–prey interactions may be influenced if both the predator and prey are treated with elevated CO_2, and any potential interaction with rising ocean temperatures. In fish, predator–prey interactions can be altered when both predator and prey are exposed to elevated CO_2 [20] and with elevated temperature [21]. Additionally, the precise effects on prey mortality rates and predator–prey dynamics will depend on how predators and prey interact together under wild conditions.

For some of the behaviours tested here, we found greater variation at elevated CO_2 compared with control conditions, suggesting that individuals differ in their tolerance to increased CO_2. Indeed in fish, variation in CO_2 tolerance results in selective mortality in the wild [22]. As selection acts upon variation within a population, the potential for adaptation through selection should be a focus of future research, especially for key ecological behaviours that have the potential to reorganize trophic dynamics in marine ecosystems.

Ethics. Research adhered to local guidelines and appropriate permissions were obtained.

Data accessibility. Data are available from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.jc77j) [17].

Authors' contributions. S.-A.W. and P.L.M. conceived the study; S.-A.W. designed the experiment, analysed the data and wrote the first draft of the manuscript; S.-A.W. and J.B.F. performed the experiments. All authors discussed the results and contributed to the final version of the manuscript. All authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We have no competing interests.

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References

1. Kroeker KJ, Kordas RL, Crim RN, Singh GG. 2010 Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* **13**, 1419–1434. (doi:10.1111/j.1461-0248.2010.01518.x)
2. Hoegh-Guldberg O, Cai R, Poloczanska ES, Brewer PG, Sundby S, Hilmi K, Fabry VJ, Jung S. 2014 The ocean. In *Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds VR Barros *et al.*), pp. 1655–1731. Cambridge, UK: Cambridge University Press.
3. Watson S-A, Lefevre S, McCormick MI, Domenici P, Nilsson GE, Munday PL. 2014 Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels. *Proc. R. Soc. B* **281**, 20132377. (doi:10.1098/rspb.2013.2377)
4. Manríquez PH *et al.* 2013 Ocean acidification disrupts prey responses to predator cues but not net prey shell growth in *Concholepas concholepas* (loco). *PLoS ONE* **8**, e68643. (doi:10.1371/journal.pone.0068643)
5. Manríquez PH, Jara ME, Mardones ML, Torres R, Navarro JM, Lardies MA, Vargas CA, Duarte C, Lagos NA. 2014 Ocean acidification affects predator avoidance behaviour but not prey detection in the early ontogeny of a keystone species. *Mar. Ecol. Prog. Ser.* **502**, 157–167. (doi:10.3354/meps10703)
6. Spady BL, Watson S-A, Chase TJ, Munday PL. 2014 Projected near-future CO_2 levels increase activity and alter defensive behaviours in the tropical squid *Idiosepius pygmaeus*. *Biol. Open* **3**, 1063–1070. (doi:10.1242/bio.20149894)
7. Rossi T, Connell SD, Nagelkerken I. 2016 Silent oceans: ocean acidification impoverishes natural soundscapes by altering sound production of the world's noisiest marine invertebrate. *Proc. R. Soc. B* **283**, 20153046. (doi:10.1098/rspb.2015.3046)
8. Dodd LF, Grabowski JH, Piehler MF, Westfield I, Ries JB. 2015 Ocean acidification impairs crab foraging behaviour. *Proc. R. Soc. B* **282**, 20150333. (doi:10.1098/rspb.2015.0333)
9. Lefevre S, Watson S-A, Munday PL, Nilsson GE. 2015 Will jumping snails prevail? Influence of near-future CO_2, temperature and hypoxia on respiratory performance in the tropical conch *Gibberulus gibberulus gibbosus*. *J. Exp. Biol.* **218**, 2991–3001. (doi:10.1242/jeb.120717)
10. Nilsson GE, Dixson DL, Domenici P, McCormick MI, Sørensen C, Watson SA, Munday PL. 2012 Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nat. Climate Change* **2**, 201–204. (doi:10.1038/nclimate1352)
11. Moya A *et al.* 2016 Near-future pH conditions severely impact calcification, metabolism and the nervous system in the pteropod *Heliconoides inflatus*. *Glob. Change Biol.* **22**, 3888–3900. (doi:10.1111/gcb.13350)
12. Briffa M, de la Haye K, Munday PL. 2012 High CO_2 and marine animal behaviour: potential mechanisms and ecological consequences. *Mar. Pollut. Bull.* **64**, 1519–1528. (doi:10.1016/j.marpolbul.2012.05.032)
13. Stella JS, Pratchett MS, Hutchings PA, Jones GP. 2011 Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Oceanogr. Mar. Biol. Annu. Rev.* **49**, 43–104.
14. Duffy JE, Hay ME. 2001 The ecology and evolution of marine consumer-prey interactions. In *Marine community ecology* (eds MD Bertness, SD Gaines, ME Hay), pp. 113–157. Sunderland, MA: Sinauer Associates.
15. Bibby R, Cleall-Harding P, Rundle S, Widdicombe S, Spicer J. 2007 Ocean acidification disrupts induced defences in the intertidal gastropod *Littorina littorea*. *Biol. Lett.* **3**, 699–701. (doi:10.1098/rsbl.2007.0457)
16. Jellison BM, Ninokawa AT, Hill TM, Sanford E, Gaylord B. 2016 Ocean acidification alters the response of intertidal snails to a key sea star predator. *Proc. R. Soc. B* **283**, 20160890. (doi:10.1098/rspb.2016.0890)
17. Watson S-A, Fields JB, Munday PL. 2016 Data from: Ocean acidification alters predator behaviour and reduces predation rate. Dryad Digital Repository. (http://dx.doi.org/10.5061/dryad.jc77j)
18. Munday PL, Dixson DL, McCormick MI, Meekan M, Ferrari MCO, Chivers DP. 2010 Replenishment of fish populations is threatened by ocean acidification. *Proc. Natl Acad. Sci. USA* **107**, 12 930–12 934. (doi:10.1073/pnas.1004519107)
19. Gaylord B *et al.* 2015 Ocean acidification through the lens of ecological theory. *Ecology* **96**, 3–15. (doi:10.1890/14-0802.1)
20. Allan BJM, Domenici P, McCormick MI, Watson S-A, Munday PL. 2013 Elevated CO_2 affects predator-prey interactions through altered performance. *PLoS ONE* **8**, e58520. (doi:10.1371/journal.pone.0058520)
21. Ferrari MCO, Munday PL, Rummer JL, McCormick MI, Corkill K, Watson SA, Allan BJM, Meekan MG, Chivers DP. 2015 Interactive effects of ocean acidification and rising sea temperatures alter predation rate and predator selectivity in reef fish communities. *Glob. Change Biol.* **21**, 1848–1855. (doi:10.1111/gcb.12818)
22. Munday PL, McCormick MI, Meekan M, Dixson DL, Watson S-A, Chivers DP, Ferrari MCO. 2012 Selective mortality associated with variation in CO_2 tolerance in a marine fish. *Ocean Acidif.* **1**, 1–5. (doi:10.2478/oac-2012-0001)