

Research



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Global change biology

Ocean acidification alters predator behaviour and reduces predation rate

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Ocean acidification poses a range of threats to marine invertebrates; however, the emerging and likely widespread effects of rising carbon dioxide (CO₂) 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 (CO₂) levels and subsequent ocean acidification affect the survival, growth, calcification and reproduction of marine organisms [1]. However, recent research shows CO₂ levels projected for the end of the century ($p\text{CO}_2 \leq 1000 \mu\text{atm}$, 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 CO₂ levels where effects on physiology are not yet manifest [3,9]. Furthermore, evidence that elevated CO₂ 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 CO₂ 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 CO₂ 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 CO₂ [3–5,15,16], but how elevated CO₂ may affect the predators of these species has not been tested. For a temperate gastropod, one recent study showed that elevated CO₂ affected the avoidance of predator cues, but not cue detection of mussel prey [5]. Here, to determine the potential effects of elevated CO₂ on predator behaviour and predation rate, we assess the effects of near-future CO₂ 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 CO₂ affects the antipredator behaviour of its prey, the humpbacked conch *Gibberulus gibberulus gibbosus* (Röding, 1798) [3], but how elevated CO₂ might affect the predator, and thus predator–prey interactions between these species, is unknown. Specifically, we investigate whether exposure to elevated CO₂ 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) CO₂ 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 CO₂ 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 CO₂ 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 CO₂ increased the distance travelled by cone snails during the 15 min trial ($t_{20} = 2.521$, $p = 0.020$; figure 1). At 975 µatm CO₂, cone snails moved three to four times further (186.0 ± 59.0 mm, mean \pm 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 CO₂ 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 CO₂ cone snails. The number of left- and right-side choices was distributed equally in control predators (54.5%); however, 81.8% of elevated CO₂ predators

finished the trial left of the starting line and one elevated CO₂ 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 CO₂ predators, whose trajectory tended to curve.

During the 15 min trial, 81.8% of control predators buried; however, only 27.3% of elevated CO₂ predators buried. Resultantly, the amount of time spent buried was greater at control (6.0 ± 1.2 min) than at elevated CO₂ 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 CO₂ 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 CO₂ conditions. In self-righting trials, nine cone snails righted in each treatment after 30 min. There was no significant difference in righting time with CO₂ ($t_{16} = 2.100$, $p = 0.052$; figure 1), although there was a trend for increased self-righting time at elevated CO₂ (16.4 ± 1.4 min, mean \pm s.e.) compared with control (11.4 ± 1.9 min) conditions.

(b) Predator–prey interactions

Elevated CO₂ increased cone snail activity during the 15 min predator–prey interaction with elevated CO₂ cone snails moving 255.1 ± 93.6 mm (mean \pm 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 CO₂ 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 CO₂ 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 CO₂ predators.

4. Discussion

Our findings show that projected end-of-century CO₂ conditions [2] affect a range of both general and hunting behaviours of predatory invertebrates, in this case a tropical predatory mollusc. Elevated CO₂ (975 µatm) increased activity by increasing the distance travelled and thus average speed by more than 3 \times 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 CO₂, similar to previous findings in fishes [18]. Elevated CO₂ did not significantly affect self-righting ability in this predator, nor (as previously found) its prey [3], although elevated CO₂ can alter self-righting time in a temperate mollusc [4].

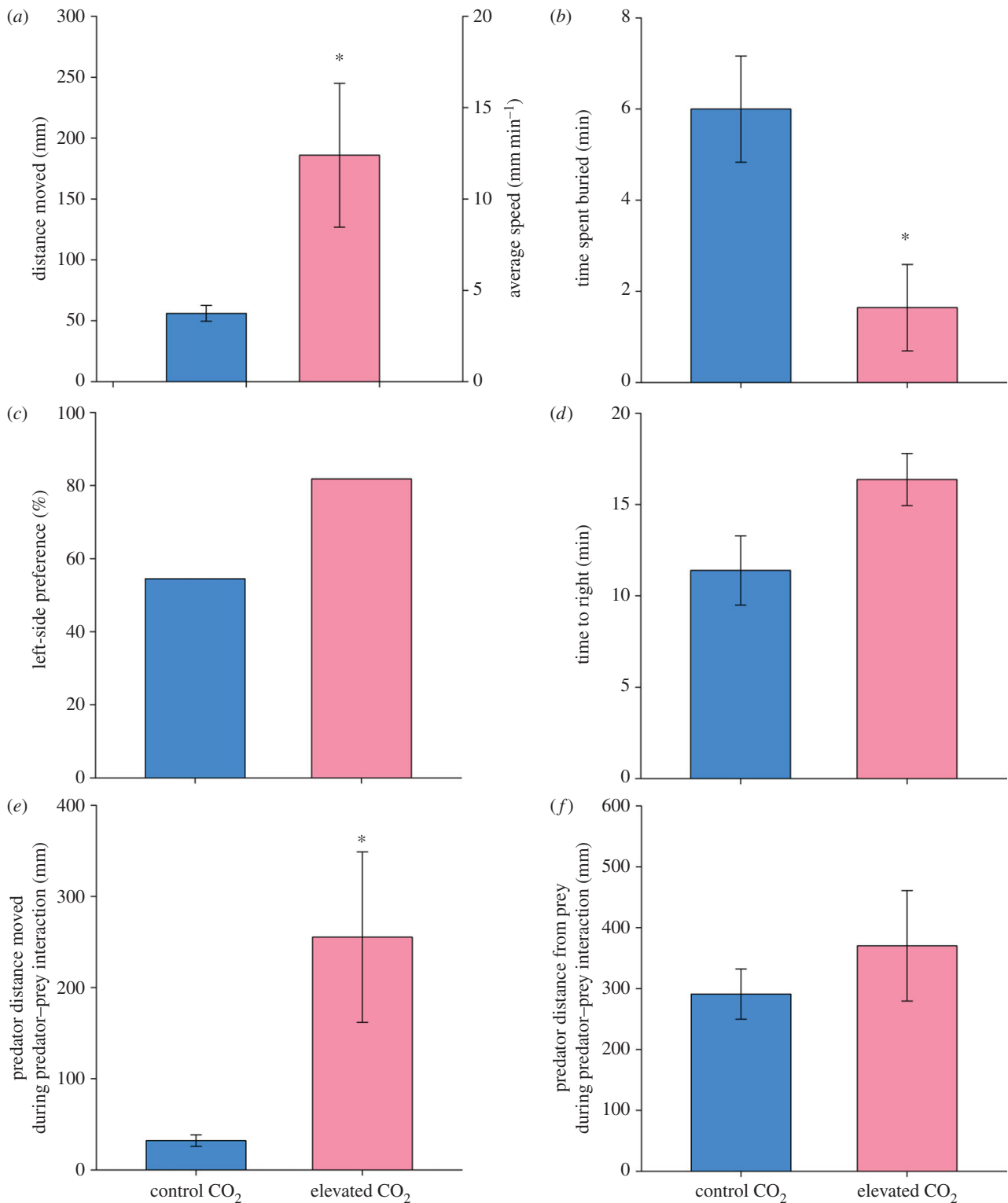


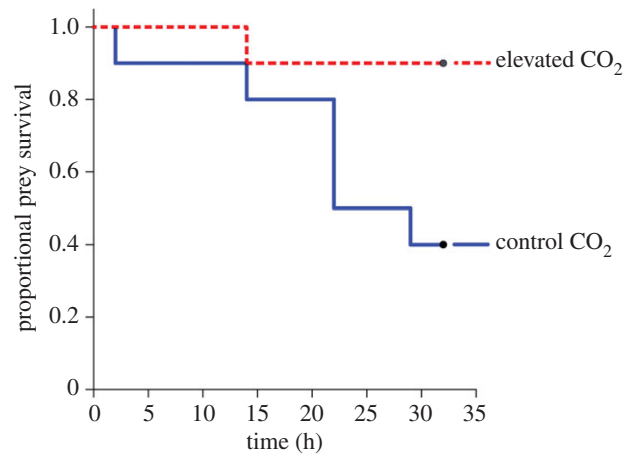
Figure 1. Effect of ocean acidification on key ecological behaviours of the predatory marbled cone snail: (a) distance travelled and speed, (b) time spent buried, (c) percentage of individuals that finished the trial on the left side of the test arena, (d) time to right; and during the 15 min predator–prey interaction in the arena: (e) distance travelled by the predator and (f) predator distance from prey. Blue and pink bars show control and elevated CO₂-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 \times) at elevated CO₂ 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 CO₂ 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 ($\mu\text{mol kg}^{-1}$ SW) | $p\text{CO}_2$ (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 \pm 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 CO₂-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 CO₂ 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 CO₂ 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 CO₂ levels are likely to make future ecosystem structure and function more difficult to predict. Increasing evidence for behavioural effects of elevated CO₂ 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 CO₂ 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 CO₂, 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 CO₂ [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 CO₂ compared with control conditions, suggesting that individuals differ in their tolerance to

increased CO₂. Indeed in fish, variation in CO₂ 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].

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