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Parental effects improve escape performance of juvenile reef fish in a high-CO$_2$ world

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Rising CO$_2$ levels in the oceans are predicted to have serious consequences for many marine taxa. Recent studies suggest that non-genetic parental effects may reduce the impact of high CO$_2$ on the growth, survival and routine metabolic rate of marine fishes, but whether the parental environment mitigates behavioural and sensory impairment associated with high CO$_2$ remains unknown. Here, we tested the acute effects of elevated CO$_2$ on the escape responses of juvenile fish and whether such effects were altered by exposure of parents to increased CO$_2$ (transgenerational acclimation). Elevated CO$_2$ negatively affected the reactivity and locomotor performance of juvenile fish, but parental exposure to high CO$_2$ reduced the effects in some traits, indicating the potential for acclimation of behavioural impairment across generations. However, acclimation was not complete in some traits, and absent in others, suggesting that transgenerational acclimation does not completely compensate the effects of high CO$_2$ on escape responses.

1. Introduction

Carbon dioxide (CO$_2$) levels in the world's oceans are increasing owing to rising atmospheric CO$_2$ concentrations [1]. Higher CO$_2$ levels are predicted to affect the physiology and behaviour of many marine species [2,3]. Exposure to elevated CO$_2$ can lead to extra- or intracellular acidosis in marine animals, with effects on growth, development and survival [4,5]. This may be particularly relevant for early life stages as the physiological costs of maintaining acid–base balance could be greater owing to the relatively large surface area to volume ratio of early life stages and less developed acid–base regulatory mechanisms [6]. Some of the most dramatic effects of elevated CO$_2$ levels reported to date are impaired sensory ability and altered behaviours of larval and juvenile fishes [3,7,8]. Behavioural effects of high CO$_2$ include changes in antipredator responses [9], olfactory [10,11] and auditory preferences [12], activity levels [13,14], behavioural lateralization [15,16] and visual risk assessment [17]. These behavioural changes affect key ecological processes, such as habitat selection [18], the timing of settlement [19] and predator–prey interactions [9,20]. The underlying mechanism linking elevated CO$_2$ to these diverse changes in behaviour is difficult to assess but appears to be interference of the acid–base regulatory process with the function of major neurotransmitter receptors in the brain [21].

While our understanding of how elevated CO$_2$ can constrain individual performance is increasing, the potential for adaptation or acclimation over climate change relevant timescales remains largely unresolved [22]. Importantly, the environmental conditions experienced by parents may affect their physiological condition and provide the opportunity for non-genetic effects to be transferred to their offspring [23,24]. Indeed, recent work has demonstrated that some of the negative physiological effects of climate change on marine organisms can be reduced if the parents have been exposed to the same environmental history as

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their offspring [25–27]. This indicates that non-genetic parental effects may alter how marine organisms respond to elevated CO_2 and provides evidence that the response to environmental stress may depend on the history of previous life stages. However, these studies have focused on physiological acclimation across generations and it is not known whether behaviour is subjected to the same rapid transgenerational acclimation.

A critical stage in the life of reef fishes is the end of the larval phase, when they settle to the benthic environment. Mortality within the first few days of settlement is variable, but uniformly high, averaging 56% for tropical reef fishes [28]. Success at this life stage is predominantly a consequence of the size, growth and escape performance of new recruits [29,30]. Escape responses consist of sudden accelerations in response to a startling stimulus, for example a predator strike, and are observed in many fish species from various taxa [31]. A successful escape response consists of finely tuned responsiveness and locomotor performance. The speed of escape and duration of response may be related to locomotor performance [32]. By contrast, the perception of a threat, response latency and directionality of escape are related to neural and sensory capacity [33–35]. The fast kinematics of the escape responses are usually controlled by the Mauthner cells which are triggered as a reaction to the fast approach of a predator, although other reticulospinal cells may also be involved [33].

Though recent studies have shown that elevated CO_2 can increase the mortality rate of prey when exposed to predators [13,14], the extent to which fish larvae can acclimate their escape responses across generations exposed to elevated CO_2 is unknown. Rearing of adults and juveniles under current-day CO_2 levels (400 µatm) or CO_2 levels projected to occur by the end of the century (1087 µatm) [36] allowed us to test the hypothesis that transgenerational acclimation may reduce the impact of elevated CO_2 on the outcome of predator–prey interactions. Comparisons between treatments allowed us to determine the acute (within-generation) effects of increased CO_2 on juvenile escape performance and to test whether such effects were mediated by exposure of parents to increased CO_2. Furthermore, by investigating a range of behavioural and locomotor variables that are critical to a successful escape response [37] we were able to test whether the capacity for acclimation to elevated CO_2 may differ between escape processes linked to locomotor performance and those more closely linked to cognitive processes.

2. Material and methods

(a) Study species and brood-stock maintenance

To examine the effect of elevated CO_2 on the escape responses of juvenile reef fish, adult breeding pairs of the cinnamon anemone fish, *Amphiprion melanopus*, were collected from the Palm Island Region of the central Great Barrier Reef, Australia (18°37′ S, 146°30′ E). Breeding pairs were housed in individual 45 l aquaria and maintained at long-term average temperatures for the collection location (22.5°C winter and 28.5°C summer). Pairs were randomly assigned to the control (400 µatm) and high (1087 µatm) CO_2 treatments in June 2011, and CO_2 was slowly adjusted to the desired level over a two-week period. This allowed pairs to be conditioned in their CO_2 treatments for five months before the start of the breeding season in November 2011. Temperatures were increased from winter temperatures of 22.5°C at a rate of 0.5°C per week until the summer breeding temperature of 28.5°C

was reached in the first week of November 2011. Breeding pairs were maintained in their CO_2 treatments until May 2012. Breeding pairs were provided with half of a terracotta pot as a shelter and a spawning site. Pairs were allowed to spawn naturally during the breeding season (November 2011–May 2012) and spawning sites were checked daily for the presence of a new egg clutch.

(b) Juvenile rearing

To examine the difference between acute exposure to CO_2 and parental effects of CO_2 on juvenile reef fish, three juvenile treatment groups were used: (i) juveniles from control parents were hatched into control CO_2 levels (control–control), (ii) juveniles from high CO_2 parents were hatched into high CO_2 (high–high) and (iii) juveniles from control parents were hatched into high CO_2 (control–high). On the night of hatching, terracotta pots with clutches were moved to 60 l larval rearing tanks and juveniles were reared in their designated CO_2 level from hatching. Tanks were filled with treated system water and aerated with premixed air to the desired CO_2 level. Juveniles were held under 13 L : 11 D regime. Aquaria were slowly flushed for 11 h overnight with fresh treatment water at the relevant CO_2 level to remove any excess food and to maintain water quality. Larvae were fed live rotifers (10 individuals ml^{-1} of tank water) and then weaned to max of 5 individuals ml^{-1} of *Artemia* spp. Fish were allowed 13 h to feed as food was administered in the morning. Fish were reared in clutch groups until 11 days posthatching at which point the juveniles are considered competent to settle. Clutches from three to four different parents per CO_2 treatment were used in the experiment to ensure genetic diversity. Offspring used in the experiments were approximately equally distributed among the three to four breeding pairs in each treatment: 29–40% per pair from three pairs in control–control, 29–37% per pair from three pairs in high–high and 21–30% per pair from four pairs in control–high. At the end of their pelagic larval phase (10–11 days posthatching), juveniles (mean SL 13.2 mm ± 0.06 s.d.) were used for escape performance analysis. We found no significant difference among the three groups with respect to standard length (SL), body depth, caudal peduncle length and tail width.

(c) Experimental system and seawater chemistry

Adult and juvenile anemone fish were reared in an environmentally controlled aquarium facility at James Cook University, Townsville, Australia. Two 8000 l recirculating seawater systems, one maintained at control CO_2 (400 µatm) and the other at elevated CO_2 (1087 µatm), supplied seawater to individual aquariums. CO_2 treatments were achieved by CO_2 dosing to a set pH following standard techniques. A pH computer (Aquamedic AT-Control, Germany) regulated CO_2 dosing in a 3000 l temperature-controlled sump within each system. Temperature (Comark C22) and pH$_{NBS}$ (Hach HQ40d) were recorded daily in the rearing tanks. Salinity and total alkalinity were measured weekly. Total alkalinity was measured by Gran titration from water samples of replicate tanks in each system. Accuracy of titrations was within 1% of certified reference material (Prof. A. Dickson, Scripps Oceanographic Institute). Average seawater pCO_2 was calculated in the program CO2SYS using the Mehrbach constants refit by [38]. Seawater parameters are presented in table 1.

(d) Experimental protocol

Juvenile fish were individually introduced into a grey circular experimental arena (diameter 250 mm; water level 100 mm) filled with water at the same CO_2 treatment as they were reared in. Shallow water depth (100 mm) was used in the experimental tank in order to minimize displacement in the vertical dimension. Fish were introduced to the arena via a water-filled

Table 1. Seawater parameters for parents and juveniles reared at control and high CO_2. Values are means $\pm$ s.d.

treatment	temp. (°C)	salinity (ppt)	total alkalinity (μmol kg^{-1} SW)	pH$_{NBS}$	pCO$_2$ (μatm)
control	28.4 $\pm$ 0.01	33.3 $\pm$ 0.12	2058.32 $\pm$ 15.81	8.15 $\pm$ 0.005	400 $\pm$ 6.33
high	28.5 $\pm$ 0.01	33.6 $\pm$ 0.09	2168.24 $\pm$ 6.70	7.81 $\pm$ 0.008	1087 $\pm$ 24.67

sample jar. This minimized any stress associated with the movement from the tank to arena. Water temperature in the experimental arena was 28.5°C. The arena was illuminated with four 150 W spotlights, placed above the water surface, by the side of the tank. One minute after being released into the experimental tank, an escape response was elicited by the release of a clear plastic cylinder with a tapered end (38.3 g, 25 mm diameter, 120 mm length) from 350 mm above the water surface. This was accomplished by turning off an electromagnet to which the cylinder was attached via a metal disc (15 mm in diameter) applied to the top end of the cylinder. In order to provide a sudden stimulation and allow calculation of the escape latency [39,40], the stimulus was released through a white PVC tube (diameter 6 cm, length 30 cm) suspended above the experimental tank, with the bottom edge at a distance of 10 mm above the water level. In order to record the frame during which the stimulus hit the water surface (i.e. stimulus onset), a small mirror (5 × 5 cm) was placed at 45° near the cylinder, above the water surface. Fish were startled more than two body lengths from the arena's edge to minimize edge effects on escape responses [41]. The area above and around the tank was screened off with polystyrene to avoid laboratory disturbances. Responses to the stimulus were filmed from above with a high-speed camera (Casio ex-fh20; 420 fps) and video recordings were analysed using IMAGEJ software. Videos were calibrated with a 5 cm line inside the tank. Fish that displayed no reaction to the stimulus were omitted from the directionality analysis leading to a slight variation between sample sizes. Sample sizes are stated in figure 1.

(e) Kinematic analysis

Escape response variables were defined as follows:

Locomotor variables

(1) Response distance (in mm) is a measure of the total distance covered by the fish from the onset to the end of the escape response (i.e. when the prey comes to a halt).
(2) Mean response speed (U_{mean} in m s^{-1}) was measured as the distance covered within a fixed time (24 ms) which corresponds to the average duration of the first two tail flips of the tail (the first two axial bends, i.e. stages 1 and 2 defined based on Domenici & Blake [31] which is the period considered crucial for avoiding predator ambush attacks [31,37].
(3) Maximum speed (U_{max} in m s^{-1}) was measured as the maximum speed reached at any time during the response.
(4) Response duration (in s) was measured as the elapsed time from the start to the end of response (i.e. when the fish came to a halt).

Non-locomotor variables

(1) Responsiveness was defined for each treatment as the proportion of animals that responded with a sudden acceleration after being startled, out of the total number of fish.
(2) Directionality: escape responses were divided into 'away' and 'towards' responses when the first detectable movement of the head was oriented away and towards the stimulus, respectively [42].

(3) Response latency (in ms) was measured as the time interval between the stimulus onset and the first detectable movement leading to the escape of the animal.

(f) Statistical analyses

The effects of CO_2 exposure on the escape responses of juvenile fish were examined using a one-way multivariate analysis of variance (MANOVA). The effect of CO_2 exposure on each locomotor variable (response distance, mean response speed, maximum response speed, response duration and latency) was further explored using an analysis of variance (ANOVA). Residual analysis was used to determine whether the data met the assumptions of normality and homogeneity of variance. Tukey's HSD post hoc tests were used to examine the differences detected by the ANOVA. The effect of CO_2 exposure on responsiveness was analysed with a χ^2 test on the count data (number of responding and non-responding fish at each treatment). Two-tailed binomial tests were performed to determine whether CO_2 exposure had an effect on directionality of response, comparing the proportion of individuals that moved away from or towards the stimulus and assuming a 0.5 probability of turning either way.

3. Results

The MANOVA revealed that escape responses were influenced by the CO_2 treatment (Pillai's trace$_{(12,212)}$ = 2.93, $p < 0.0001$). ANOVA detected significant differences in four out of the six variables tested (distance travelled, mean response speed, maximum response speed and response duration).

(a) Locomotor variables

The response distance following stimulation was significantly shorter in the control–high group compared with the control–control group demonstrating an acute effect of high CO_2 on distance travelled (figure 1a; $F_{2,122} = 4.135$, $p = 0.018$). By contrast, there was no significant difference between the high–high group and the control–control group (Tukey's test, $p = 0.6$), demonstrating a parental effect on distance travelled in the high–high group. However, the distance travelled by the high–high group was intermediate to the control–control group and control–high group (figure 1a), indicating that exposing parents to high CO_2 did not completely reduce the effect of high CO_2 on response distance.

The mean response speed during an escape response differed significantly among the groups (figure 1b; $F_{2,122} = 4.13$, $p = 0.01$). Response speed was significantly less in the control–high group when compared with the control–control group demonstrating an acute effect of elevated CO_2 on escape speed (Tukey's test, $p = 0.03$). There was no significant difference in response speed between the high–high group and the control–control group (Tukey's test $p = 0.3$). Nevertheless, the response speed exhibited by the high–high group was intermediate to the control–control group and control–high group (figure 1b), indicating that parental exposure to
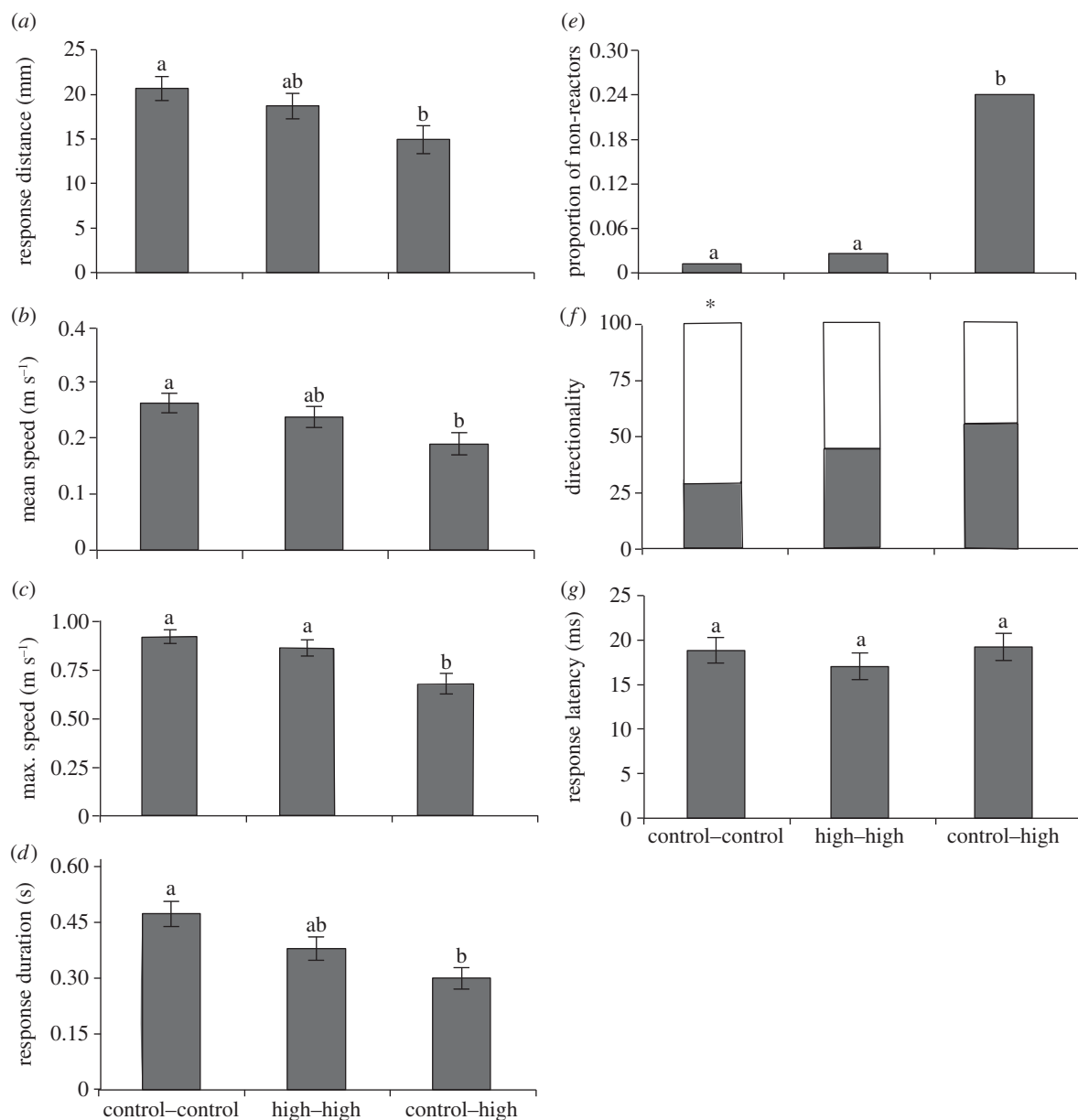
Figure 1. The effect of elevated CO_2 on the escape performance of juvenile *A. melanopus* in three different parent – offspring CO_2 treatments (control – control, high – high and control – high). The comparison between control – control and control – high assesses acute effects of elevated CO_2 on juveniles, while the comparison of the high – high group with the other two groups assesses the effects of parental exposure to high CO_2 on juvenile performance. Variables displayed are: (a) response distance, (b) mean speed, (c) max. speed, (d) response duration, (e) proportion of non-reactors, (f) directionality and (g) response latency. Errors are standard errors. Letters above bars represent Tukey's HSD groupings of means. Asterisk above panel (f) represents the proportion of responses directed away (unfilled portion) and towards (filled portion) the stimulus that differed significantly from random. n = control – control 45, high – high 37, control – high 43 (a–e); n = control – control 46, high – high 34, control – high 34 (f,g).

high CO_2 was not sufficient enough to fully reduce the negative effects of CO_2 exposure on response speed in juveniles.

The maximum response speed was significantly less in the control–high group compared with the control–control and high–high groups (figure 1c; $F_{2,122} = 6.995$, $p = 0.001$) demonstrating an acute effect of CO_2 treatment on the maximum speed achieved. However, there was no difference in maximum response speed between the control–control group and the high–high group (Tukey's test $p = 0.7$, figure 1c), indicating that parental effects had completely reduced the negative effects of high CO_2 on maximum response speed in juveniles.

The duration of the burst response following stimulation (response duration) was significantly shorter in the control–high group compared with the control–control group demonstrating an acute effect of high CO_2 on response

duration (figure 1d; $F_{2,122} = 7,78$, $p < 0.001$). By contrast, there was no significant difference between the high–high group and the control–control group, suggesting a parental influence on response duration in the high–high group (Tukey's test $p = 0.09$). However, the response duration exhibited by the high–high group was intermediate to the control–control group and control–high group (figure 1d), indicating that parental effects did not completely reduce the acute effect of high CO_2 on distance travelled.

(b) Non-locomotor variables

The proportion of juveniles that displayed no reaction to the stimulus was significantly greater in the control–high group compared with the control–control group ($\chi^2 = 5.16$, d.f. = 1, $p = 0.023$) and the high–high group ($\chi^2 = 4.09$, d.f. = 1,

$p = 0.043$), demonstrating a clear negative effect of acute CO_2 exposure on reactivity to the stimulus (figure 1e). The high–high group was not significantly different from the control–control group ($\chi^2 = 0.27$, d.f. = 1, $p = 0.6$), suggesting that parental exposure to elevated CO_2 completely restored reactivity in juveniles exposed to elevated CO_2.

Exposure to high CO_2 had a detrimental effect on the directionality of the escape response. In the control–control group, 72% of the escape responses were away from the stimulus. By contrast, only 45% of respondents turned away from the stimulus in the control–high group. The direction turned by the high–high group was intermediate to the control–control group and control–high group (figure 1f). The proportion of responses directed away and towards the stimulus differed significantly from random (50 : 50) for the control–control group (figure 1f; $n_{norm} = 46$, $p = 0.001$), but not for the other two treatments (high–high, figure 1f: $n_{norm} = 34$, $p = 0.1$; control–high, figure 1f: $n_{norm} = 34$, $p = 0.1$). Directionality differed among treatments ($\chi^2 = 6.32$, d.f. = 2, $p = 0.042$). Specifically, directionality differed between the control–control and the control–high groups ($\chi^2 = 6.63$, d.f. = 1, $p = 0.01$). However, the control–control and the high–high groups ($\chi^2 = 2.70$, d.f. = 1, $p = 0.1$) and the control–high and the high–high groups were not significantly different ($\chi^2 = 0.9$, d.f. = 1, $p = 0.3$). Overall, these results suggest that CO_2 affected directionality and that parental exposure to a high CO_2 environment partially reduces this effect. However, individuals whose parents were exposed to elevated CO_2 exhibited a directionality that does not differ from random. Latency was not affected by any of the CO_2 treatments (figure 1g; $F_{2,112} = 1.63$, $p = 0.19$).

4. Discussion

Elevated CO_2 can lead to changes in growth, survival, routine metabolic rate [26,43], behaviour [10–15] and predator–prey interactions [9,20] of reef fish. Here, we demonstrate that CO_2 concentrations that are predicted for the end of this century adversely affected the escape-response performance of juvenile fish. In the control–high treatment, there was a significant increase in the number of fish that did not initiate an escape response compared with control–control group, and negative effects on distance travelled, mean response speed, maximum response speed and response duration were observed. This demonstrates that exposure of juvenile fish to elevated CO_2 has a highly significant effect on the kinematics of the escape response that is likely to impact on the ability of prey to avoid predators [37]. However, negative effects of high CO_2 exposure on escape responses were greatly reduced or absent in the high–high group, with fish showing similar performance levels found in the control–control group for some traits. This result is important because it indicates that transgenerational acclimation can help to overcome behavioural impairment observed in fishes exposed to high CO_2. As CO_2 levels rise over coming decades, both parental and offspring generations will experience similar elevated CO_2 levels; thus our results indicate that this parental exposure will help to reduce some of the negative effects of high CO_2 on behaviour.

While parental effects moderated the impacts of high CO_2 on most of the escape-response traits measured, performance was intermediate between control–control and control–high treatment groups for over half the traits examined. This indicates that although parental effects may be beneficial, they may not fully restore performance in many instances and some negative effects of high CO_2 on escape performance will remain. Furthermore, while some responses by juveniles, for example proportion of non-reactors, were completely reduced by exposing parents to high CO_2, other responses, for example the direction of response, were not improved. Consequently, our results demonstrate that transgenerational acclimation of behaviour to high CO_2 can be complete, partial or absent and that the magnitude of acclimation can vary markedly among behavioural responses.

Recent research suggests that cognitive impairment in fishes exposed to elevated CO_2 is owing to the interference of acid–base regulatory process with the functioning of brain neuroreceptors [21]. Given this, it is not surprising that directionality was affected in the fish exposed to elevated CO_2. Directionality is an important trait and an early mistake, as turning towards a predator, may increase the risk of capture [35,44]. Although transgenerational acclimation improved performance in this particular trait, individuals whose parents were exposed to elevated CO_2 exhibit a directionality that does not differ from random, likely owing to an impairment of the sensory-motor system. Consequently, exposure to elevated CO_2 could have a significant effect on the outcome of the predator–prey interactions, even if parents have been exposed to similar CO_2 levels. This contrasts with the behavioural acclimation seen with responsiveness, which highlights the specific nature of behavioural acclimation. Interestingly, elevated CO_2 had no effect on escape latency, which has also been observed in fish exposed to hypoxia suggesting that decreased oxygen may impair the sensory mechanisms involved in the detection of the mechano-acoustic signal. However, as long as the response threshold is reached, the time course to initiate the response does not appear to be affected [34].

We found that almost all locomotory variables were affected following acute CO_2 exposure. More specifically, there were reductions in the distance travelled, mean response speed, maximum response speed and response durations. The indirect mechanism underlying this response could be a decline in aerobic scope caused by an increase in resting metabolic rate after short-term exposure to elevated CO_2 [43]. This effect may be similar to the observed reduction in escape swimming performance observed in hypoxia, which has been attributed to a trade-off between physiological exhaustion requiring energy saving, and the need to escape from a predatory attack [34]. Because the anaerobic burst is eventually paid off by excess post-exercise oxygen consumption, fish with reduced metabolic scope under elevated CO_2 conditions may therefore show low-performance escapes as an energy-saving strategy. In addition, reduced aerobic scope may have caused a decrease in burst swimming performance indirectly, i.e. as a result of reduced condition [26]. Notably, the negative effects of CO_2 exposure on all locomotory variables were less apparent if the parents had been exposed similarly. This suggests that transgenerational acclimation may play a major role not only in juvenile development and metabolism [26], but also in important locomotory behaviour, for example escape performance. Previous work has demonstrated that various physiological parameters (i.e. routine metabolic rate, growth and survival) are improved in juvenile fish that have been exposed to

elevated CO_2, providing the parents have been exposed to a similar environment [26]. The restoration of routine metabolic rate seen in Miller *et al.* [26] could explain why we see an improvement in locomotory capabilities. Energy saved through improved cellular processes simply means more energy is available to escape predation.

Transgenerational plasticity (acclimation) occurs in a diverse group of taxa, such as plants [45], insects [46,47], bryozoans [48], shellfish [49] and fish [27], leading to changes in morphology [46,47], dispersal potential [48] and growth rates [27,49]. Recently, it has been observed to occur in response to environmental stressors, such as hypoxia [50], elevated temperature [25,27] and elevated CO_2 [26,49], suggesting that transgenerational acclimation may be an important mechanism in helping taxa to cope with climate change. For example, Salinas & Munch [27] found that sheepshead minnows (*Cyprinodon variegatus*) reared under high or low temperatures had optimal growth provided their parents had been exposed to similar temperatures. While our results are consistent with growing evidence for the potential importance of transgenerational acclimation in enabling organisms to cope with rapid climate change, they also demonstrate that such acclimation has limits and that not all traits will be beneficially influenced by parents being exposed to the same environmental conditions as their offspring.

We have demonstrated that there is a potential for rapid acclimation for many variables that influence escape performance, if the parents have been exposed to the same environmental history. However, parental effects did not fully restore performance in most traits. Thus, negative effects of higher CO_2 levels on behaviour remain, although at reduced levels. Whether behaviours could be fully acclimated in future generations and the potential costs of such acclimation to other processes is not yet known. This highlights the need to exercise caution when making statements about whole-organism acclimation. It remains to be seen whether these non-genetically inherited parental effects will be extended into future generations, thus potentially reducing the effects of rising CO_2 levels on populations, communities and ecosystems.

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