

# Parental environment mediates impacts of increased carbon dioxide on a coral reef fish

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**Carbon dioxide concentrations in the surface ocean are increasing owing to rising CO<sub>2</sub> concentrations in the atmosphere<sup>1</sup>. Higher CO<sub>2</sub> levels are predicted to affect essential physiological processes of many aquatic organisms<sup>2,3</sup>, leading to widespread impacts on marine diversity and ecosystem function, especially when combined with the effects of global warming<sup>4–6</sup>. Yet the ability for marine species to adjust to increasing CO<sub>2</sub> levels over many generations is an unresolved issue. Here we show that ocean conditions projected for the end of the century (approximately 1,000  $\mu$ atm CO<sub>2</sub> and a temperature rise of 1.5–3.0 °C) cause an increase in metabolic rate and decreases in length, weight, condition and survival of juvenile fish. However, these effects are absent or reversed when parents also experience high CO<sub>2</sub> concentrations. Our results show that non-genetic parental effects can dramatically alter the response of marine organisms to increasing CO<sub>2</sub> and demonstrate that some species have more capacity to acclimate to ocean acidification than previously thought.**

Increased CO<sub>2</sub> can affect acid–base regulation, oxygen transport and metabolic rate<sup>2,3,7</sup>, with consequences for individual growth, survival and reproduction. Increased temperature also affects growth and survival of marine organisms, primarily through limitations to oxygen transport<sup>5</sup>. In fish, a declining capacity for oxygen delivery to the tissues with increasing temperature sets the limits for individual performance, which ultimately determines the viability of local populations<sup>8–10</sup>. Although both increased CO<sub>2</sub> and higher temperature can constrain individual performance, a major limitation to predicting the effects of increasing CO<sub>2</sub> concentrations on marine species and ecosystems is the lack of information on acclimation or adaptation to increased CO<sub>2</sub> over timescales relevant to climate change predictions<sup>11,12</sup>. There is increasing evidence that the capacity for acclimation to environmental stress may depend on the history of previous life stages<sup>13,14</sup>. For example, recent studies show that the aerobic capacity of some thermally sensitive fish can fully acclimate to warmer water, but only if their parents have experienced the same increase in temperature<sup>15,16</sup>. Whether parental effects can similarly mediate the effects of increased CO<sub>2</sub>, or the interacting effects of increased CO<sub>2</sub> and temperature, is unknown.

We conditioned adult anemonefish, *Amphiprion melanopus*, to present-day (control, 430  $\mu$ atm) and increased-CO<sub>2</sub> treatments (moderate, 581  $\mu$ atm; high, 1,032  $\mu$ atm) consistent with projections for CO<sub>2</sub> concentrations in the atmosphere and ocean over the next 50–100 years<sup>17</sup>. Breeding pairs were allowed to spawn naturally in their CO<sub>2</sub> treatments and their offspring reared in a cross-factored CO<sub>2</sub> × temperature design. Juveniles from control parents were reared at either control CO<sub>2</sub> (control–control CO<sub>2</sub>) or transferred to high CO<sub>2</sub> (control–high CO<sub>2</sub>) at each of three temperatures (28.5 °C, 30.0 °C and 31.5 °C). Rearing temperatures represent the

present-day average summer temperature for the study population (28.5 °C) and the 1.5–3.0 °C increase in tropical sea surface temperature predicted for the next 50–100 years<sup>18</sup>. Juveniles from parents in the moderate- and high-CO<sub>2</sub> treatments were reared in similar CO<sub>2</sub> conditions as their parents (moderate–moderate CO<sub>2</sub> and high–high CO<sub>2</sub>) at each of the three temperatures (see Supplementary Table S1 for all seawater parameters). Comparisons between treatments allowed us to determine the acute (within-generation) effects of increased CO<sub>2</sub> and temperature on juvenile performance and to test if such effects were mediated by exposure of parents to increased CO<sub>2</sub>.

Standard length (SDL) and mass of fish at the end of the experiment were significantly less in the control–high CO<sub>2</sub> group compared with the control–control group at all three temperatures (SDL:  $F_{16,470} = 18.4$ ,  $P < 0.0001$ ; weight:  $F_{16,470} = 18.08$ ,  $P < 0.0001$ ; Fig. 1a,b), demonstrating a clear effect of high CO<sub>2</sub> on juvenile growth. However, these effects were absent, or reversed, when both parents and juveniles experienced increased CO<sub>2</sub> (Fig. 1a,b). SDL of juveniles in the moderate–moderate CO<sub>2</sub> and high–high CO<sub>2</sub> treatments was not significantly different from control–controls at 28.5 °C and 30.0 °C, or at 31.5 °C for the high–high CO<sub>2</sub> group (Fig. 1a). At 31.5 °C, SDL of juveniles in the moderate–moderate CO<sub>2</sub> group was less than in the control–control group, but they were still significantly larger than the control–high CO<sub>2</sub> group (Fig. 1a).

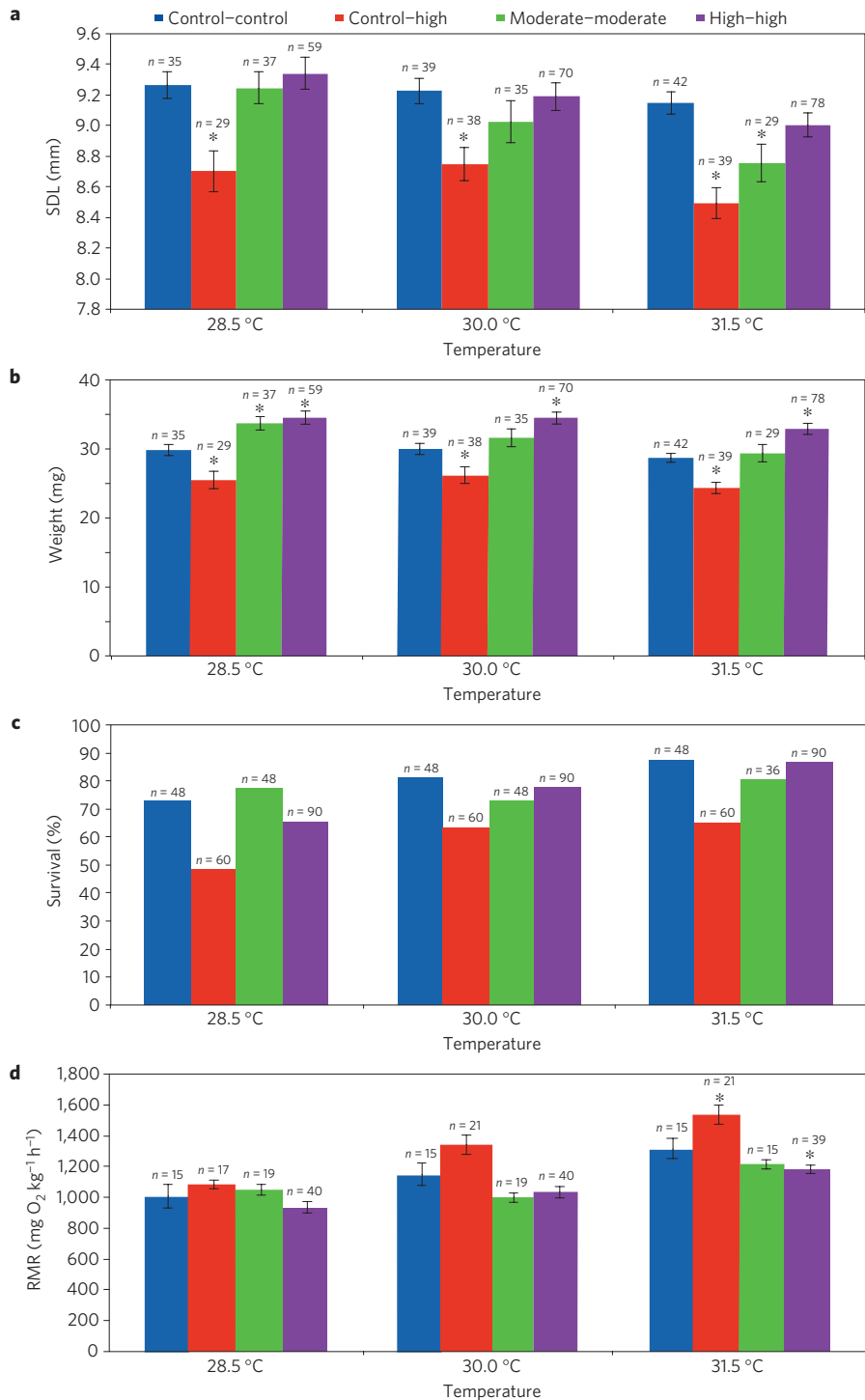
Weight in the moderate–moderate CO<sub>2</sub> and high–high CO<sub>2</sub> treatments was greater than in the control–control group, although the magnitude of the effect declined with increasing temperature (Fig. 1b). Weight of both moderate–moderate CO<sub>2</sub> and high–high CO<sub>2</sub> treatments was greater than in the control–control group at 28.5 °C, but only the high–high CO<sub>2</sub> group exhibited significantly greater mass than controls at 30.0 °C and 31.5 °C. Increased weight in the increased-CO<sub>2</sub> groups may be owing to the higher feeding rate in juvenile anemonefish exposed to increased CO<sub>2</sub> that has previously been observed<sup>19</sup>. The comparisons of length and weight among treatments demonstrate that within-generation effects of high CO<sub>2</sub> on juvenile growth are highly dependent on the CO<sub>2</sub> environment experienced by their parents.

Juvenile survival was also affected by CO<sub>2</sub> and parental treatments. Survival in the control–high CO<sub>2</sub> group was lower than the control–control group at all temperatures (Wald statistic<sub>3</sub> = 43.22,  $P < 0.001$ ; Fig. 1c). In contrast, there was no significant difference in survival between the control–control group and either the moderate–moderate or high–high CO<sub>2</sub> group (Fig. 1c), demonstrating that parental effects mediate the effect of high CO<sub>2</sub> on juvenile survival.

As expected, temperature had an independent effect on SDL ( $F_{2,470} = 8.9$ ,  $P < 0.001$ ) and weight ( $F_{2,470} = 3.7$ ,  $P < 0.05$ ),

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**Figure 1 | The effect of parental environment on life history and metabolic traits of juvenile anemonefish exposed to high CO<sub>2</sub>.** SDL (a) weight (b) survival (c) and RMR (d) of 31-day-old juveniles in three different parent-offspring CO<sub>2</sub> treatments (control-high, moderate-moderate, high-high) were compared with a control-control treatment, where both parents and offspring experienced control conditions. A significant difference between a treatment group and the control-control group is indicated with an asterisk.

with both SDL and weight declining with increasing temperature (Fig. 1a,b). The declines in SDL and weight were most apparent between 30.0 °C and 31.5 °C for all CO<sub>2</sub> treatments. The additional decline in SDL and weight associated with temperature in the control-high CO<sub>2</sub> group indicates that the acute (within-generation) effects of higher temperature and increased CO<sub>2</sub> are additive. There was no effect of temperature on survival (Wald statistic<sub>3</sub> = 4.15,  $P = 0.13$ ). Length and weight of juveniles

also varied among clutch (nested within CO<sub>2</sub> treatment; length:  $F_{16,470} = 18.4$ ,  $P < 0.0001$ ; weight:  $F_{16,470} = 18.08$ ,  $P < 0.0001$ ).

The within- and between-generation effects of increased CO<sub>2</sub> on the growth and survival of juvenile fish were associated with changes in metabolic rate. As expected, routine metabolic rate (RMR; see Supplementary Information) of 31-day-old juveniles increased with rearing temperature (Fig. 1d;  $F_{2,219} = 26.495$ ,  $P < 0.0001$ ). RMR also increased under increased CO<sub>2</sub> ( $F_{3,219} = 7.952$ ,  $P < 0.0001$ ),

but not consistently across temperature treatments. There was no difference in RMR between control–control and control–high CO<sub>2</sub> groups at 28.5 °C, but the transfer from control to high CO<sub>2</sub> significantly increased RMR at 31.5 °C (Fig. 1d). Consequently, juveniles in the control–high CO<sub>2</sub> group exhibited a greater increase in oxygen consumption between 28.5 °C and 31.5 °C ( $Q_{10} = 3.2$ ) than juveniles in the control–control group ( $Q_{10} = 2.6$ ). In contrast, juveniles in the moderate–moderate and high–high CO<sub>2</sub> groups exhibited a marked reduction in RMR compared with juveniles in the control–high CO<sub>2</sub> group (Fig. 1d). RMR of these two groups was similar to the control–control group at 28.5 °C and 30.0 °C and for the high–high CO<sub>2</sub> group was marginally lower than the control–control group at 31.5 °C (Fig. 1d;  $Q_{10} = 1.7$  moderate–moderate CO<sub>2</sub> and 2.2 high–high CO<sub>2</sub>). This demonstrates that parental effects can completely compensate for the effects of high CO<sub>2</sub> on juvenile metabolic rate.

Our results show that under CO<sub>2</sub> concentrations that could occur in the ocean by the end of this century the energy required for basic maintenance and activity (RMR) in a coral reef fish is increased. Furthermore, increased CO<sub>2</sub> had a greater influence on RMR at temperatures beyond those normally experienced by the population, thereby exacerbating the effects of rising temperature on oxygen demand. Changes in the energy budget caused by increased RMR in the control–high CO<sub>2</sub> group are reflected in patterns of somatic growth, with fish in this treatment both shorter and lighter than control–control fish after 31 days. Juvenile survival was also significantly reduced in juvenile fish exposed to high CO<sub>2</sub>. Consequently, there seems to be a link between changes in basal energy turnover and individual performance. Although such associations between the physiological effects of increased CO<sub>2</sub> and whole-organism life-history traits have been predicted<sup>2,12</sup>, they have not previously been demonstrated for marine fish.

Notably, the adverse effects of increased CO<sub>2</sub> on RMR, growth and survival did not occur when parents were exposed to the same CO<sub>2</sub> conditions as the juveniles. The conditions experienced by adults can have significant carry-over effects on the performance of their offspring<sup>13,15,20</sup>, often leading to improved capacity to cope with environmental stress<sup>21,22</sup>. However, with the exception of one recent study on oysters<sup>14</sup>, this important mechanism has not been investigated in research on ocean acidification. Many studies have reported negative effects of near-future CO<sub>2</sub> and pH levels on the early life-history stages of marine species<sup>6,23–25</sup>, including larval fish<sup>26,27</sup>. Our results clearly show that non-genetic parental effects have a highly significant influence on the performance of juvenile fish exposed to high CO<sub>2</sub>, with the potential to fully compensate for metabolic and life-history effects caused by acute (within-generation) exposure to increased CO<sub>2</sub>.

Parental effects were equally effective in moderating the acute effects of high CO<sub>2</sub> on juvenile performance at moderate (581  $\mu$ atm) and high (1,032  $\mu$ atm) CO<sub>2</sub> concentrations. In both of these future CO<sub>2</sub> scenarios, where adults experienced the same CO<sub>2</sub> conditions as their offspring, the patterns of growth, survival and RMR of juveniles were similar to the control–control group. This suggests that parental effects prepare juveniles for similar conditions to those experienced in the parental generation. Although CO<sub>2</sub> levels in the atmosphere and ocean are rising rapidly<sup>1</sup>, most species will experience a gradual increase in CO<sub>2</sub> over several generations. Consequently, parental effects could be highly effective in moderating the impacts of ocean acidification from increasing CO<sub>2</sub> concentrations over the coming decades.

Non-genetic parental effects may have a molecular (for example, epigenetic inheritance) or nutritional (for example, maternal provisioning) basis<sup>20</sup>. There was no difference in size at hatching between any of the treatments ( $F_{82,718} = 0.886, P = 0.75$ ) that would be indicative of differences in maternal provisioning. Furthermore, maternal provisioning could not account for the underlying

improvement in RMR of juveniles from parents reared in high CO<sub>2</sub>. More efficient acid–base regulatory processes and/or mitochondrial function could explain the dramatic improvement in juvenile RMR in the high–high CO<sub>2</sub> group and the corresponding improvement in growth and survival of juveniles from high-CO<sub>2</sub> parents. Transgenerational epigenetic inheritance<sup>28</sup> is a probable mechanism by which changes in gene expression for key enzymes involved with acid–base regulation or mitochondrial metabolism could be passed between generations, thereby enabling developing juveniles to improve their performance in a high-CO<sub>2</sub> environment. A previous study<sup>29</sup> found that gene expression for the major ion transporters (Na<sup>+</sup>/HCO<sub>3</sub><sup>-</sup> and Cl<sup>-</sup>/HCO<sub>3</sub><sup>-</sup>) in fish gills involved with acid–base regulation is initially downregulated following exposure to high CO<sub>2</sub>, but then returns to predisturbance levels, or is upregulated, over a period of 4–6 weeks. Na<sup>+</sup>–K<sup>+</sup>–ATPase capacity, which is expected to be the main enzyme driving the ion transport process, is also upregulated on similar timescales. Such changes in the epigenetic state of parents exposed to high CO<sub>2</sub> may prime their offspring to develop more efficient physiological pathways for a high-CO<sub>2</sub> environment. Regardless of the precise mechanism involved, our results show that the parental environment has a highly significant influence on the performance of offspring in high-CO<sub>2</sub> conditions.

Although no life-history costs of parental effects were identified here, it is possible that they exist, potentially affecting traits such as maximum size or longevity<sup>15</sup>. Furthermore, although conditioning parents to high CO<sub>2</sub> had a positive effect on the performance of juvenile *A. melanopus*, parental effects could be negative in other circumstances. For example, there would probably be consequences for juvenile growth and survival if mothers exposed to high CO<sub>2</sub> experience energetic constraints that lead to a reduction in egg provisioning<sup>13,30</sup>. We predict that parental effects are most likely to be positive for fish and other organisms with well-developed mechanisms for acid–base regulation that allow them to cope with increased CO<sub>2</sub> and where there is little evidence that exposure of adults to near-future CO<sub>2</sub> levels has significant energetic costs<sup>3,31</sup>.

Our observation of decreased SDL and weight in 31-day-old juvenile *A. melanopus* contrasts with the lack of negative effects at similar CO<sub>2</sub> levels in 11-day-old larval *Amphiprion percula*<sup>32,33</sup>. Previous experiments with *A. percula* have focused on the larval stage, during which time the fish had a continuous supply of food and were able to feed *ad libitum*. The continuous supply of food may provide the larvae with sufficient energy to overcome any detrimental effects of increased CO<sub>2</sub> on growth. In contrast, juveniles in this experiment were fed a fixed ration once a day after they passed the larval phase. The reduced access to food by juveniles, compared with earlier studies with larvae, may have allowed the effects of increased CO<sub>2</sub> on growth to become apparent. The fixed ration may also have contributed to the decline in SDL and weight at the highest temperature (31.5 °C) because RMR increased most markedly at this temperature, indicating an increase in the energetic cost of maintenance.

Publications on the impacts of ocean acidification on marine organisms are increasing exponentially; however most studies are short term and almost none consider more than one generation. Research into the effects of ocean acidification is set to increase even further in coming years owing to targeted financial support for research by national governments and international consortiums. Our results show that parental effects can have a highly significant influence on the performance of marine organisms under conditions simulating future ocean acidification. Such effects will need to be considered to make robust predictions about future impacts on marine diversity and ecosystem function.

## Methods

**Study species and brood-stock maintenance.** To examine the potential for transgenerational acclimation to ocean acidification, adult breeding pairs of the

cinnamon anemonefish, *A. 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 60-litre aquaria and maintained at control temperatures (22.5 °C winter and 28.5 °C summer). Ten breeding pairs were randomly assigned to each of the three CO<sub>2</sub> treatments (control, ~430 µatm; moderate, ~581 µatm; and high, ~1,032 µatm) at the end of August 2010 and pH was slowly adjusted to the desired levels over a two-week period (For further information on water parameters refer to the Supplementary Information). This allowed pairs to be conditioned in their CO<sub>2</sub> treatments for two months before the start of the breeding season in November. Temperatures were increased from winter temperatures of 22.5 °C at a rate of 0.5 °C per week until the summer breeding temperature, 28.5 °C, was reached in the first week of November 2010. Breeding pairs were maintained in their CO<sub>2</sub> treatments until May 2011. Breeding pairs were provided with half of a terracotta pot as a hide and a spawning site. Pairs were allowed to spawn naturally during the breeding season (November 2010–May 2011) and spawning sites were checked daily for the presence of a new egg clutch.

**Juvenile rearing.** Juveniles were reared in the designated CO<sub>2</sub> level from hatching. On the night of hatching, terracotta pots with clutches were moved to 60-litre larval rearing tanks. Tanks were filled with treated system water and aerated with premixed air to the desired level<sup>32</sup>. To examine the difference between acute exposure to CO<sub>2</sub> and parental effects of CO<sub>2</sub> on juvenile reef fish, the juveniles were either hatched into the parental CO<sub>2</sub> treatment, or some clutches from control parents were hatched into high-CO<sub>2</sub> treatment. The four juvenile CO<sub>2</sub> treatment groups are therefore named by both their parental CO<sub>2</sub> and by the CO<sub>2</sub> that they have spent their post-hatching life in, that is, control–control, control–high, moderate–moderate and high–high. Between four and eight different clutches per CO<sub>2</sub> treatment were used in the experiment, depending on the number of parents that reproduced successfully at each CO<sub>2</sub> level (control–control, four; control–high, five; moderate–moderate, four; high–high, eight). A subsample of newly hatched larvae was taken from each clutch to estimate size at hatching. The remaining juveniles were reared using standard protocols<sup>32</sup> in clutch groups until the end of the pelagic larval stage at 11 days post hatching. At the end of their pelagic larval phase a total of 45 juveniles from each clutch were randomly selected and assigned to the three temperature treatments (28.5 °C, 30.0 °C and 31.5 °C) within their CO<sub>2</sub> treatment group (*N* = 15 per temperature). Juveniles were transferred to 1.5-litre aquaria where they were reared individually at the required CO<sub>2</sub> level × temperature treatment for a further 21 days. Juveniles were fed equal rations once a day of *Artemia* spp. and INVE pellets. After 21 days, five juveniles from each CO<sub>2</sub> × temperature treatment, from each clutch, were selected to have their RMR (see Supplementary Methods) determined. All surviving juveniles were then euthanized and preserved in 4% phosphate buffered formaldehyde before being weighed and photographed to determine their SDL at a later date.

**Statistical analysis.** Partially nested factorial analyses of variance were used to compare SDL, weight and RMR among CO<sub>2</sub> treatments and temperature, with the egg clutch nested within the CO<sub>2</sub> treatment. Fisher's least significant difference post-hoc tests were used to compare treatment means. Specifically, the mean of each CO<sub>2</sub> treatment (control–high, moderate–moderate, high–high) was compared with the mean of the control–control. The frequency of survival was compared among CO<sub>2</sub> and temperature treatment using logistic regression. As the sample size for each CO<sub>2</sub> × temperature treatment for each clutch was small (*N* = 15), it was not possible to include clutch in the survival analysis and the data were pooled for this analysis. All data analysis was conducted using StatisticaX (Statsoft).

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## Author contributions

G.M.M. and P.L.M. designed the experiments. G.M.M. carried out all experimentation and analysed raw data. S.-A.W. and G.M.M. collected and analysed seawater chemistry parameters. P.L.M., G.M.M., J.M.D., S.-A.W. and M.I.M. wrote the article. All authors contributed intellectual input, read and approved the manuscript.

## Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/natureclimatechange](http://www.nature.com/natureclimatechange). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to G.M.M.