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Behavioural impairment in reef fishes caused by ocean acidification at CO_2 seeps

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Experiments have shown that the behaviour of reef fishes can be seriously affected by projected future carbon dioxide (CO_2) concentrations in the ocean[1–4]. However, whether fish can acclimate to elevated CO_2 over the longer term, and the consequences of altered behaviour on the structure of fish communities, are unknown. We used marine CO_2 seeps in Papua New Guinea as a natural laboratory to test these questions. Here we show that juvenile reef fishes at CO_2 seeps exhibit behavioural abnormalities similar to those seen in laboratory experiments. Fish from CO_2 seeps were attracted to predator odour, did not distinguish between odours of different habitats, and exhibited bolder behaviour than fish from control reefs. High CO_2 did not, however, have any effect on metabolic rate or aerobic performance. Contrary to expectations, fish diversity and community structure differed little between CO_2 seeps and nearby control reefs. Differences in abundances of some fishes could be driven by the different coral community at CO_2 seeps rather than by the direct effects of high CO_2. Our results suggest that recruitment of juvenile fish from outside the seeps, along with fewer predators within the seeps, is currently sufficient to offset any negative effects of high CO_2 within the seeps. However, continuous exposure does not reduce the effect of high CO_2 on behaviour in natural reef habitat, and this could be a serious problem for fish communities in the future when ocean acidification becomes widespread as a result of continued uptake of anthropogenic CO_2 emissions.

There is growing concern that rising CO_2 levels and ocean acidification will have profound impacts on marine biodiversity and the function of marine ecosystems[5]. However, most evidence for negative effects of ocean acidification comes from short-term laboratory experiments on single species. Very little is known about the effects of ocean acidification on ecological processes in complex communities[6,7] and efforts to develop community or ecosystem models are confounded by variation in sensitivity to acidification among similar species[8,9]. Furthermore, there is increasing evidence that some species can adjust to high CO_2 levels over the longer term[10–13]. Consequently, our ability to predict the impacts that ocean acidification will have on marine communities remains limited.

Recent experiments have shown that dissolved CO_2 levels projected for the ocean this century impair sensory systems and alter the behaviour of reef fishes. The ability to distinguish between ecologically important olfactory cues is lost[1], and juvenile fish become attracted to odours they normally avoid, such as the smell of predators[2]. Decision-making is impaired[14,15] and associative learning of predator threats no longer occurs[16]. Furthermore, juvenile fish become more active when reared at CO_2 levels projected for the near future, and exhibit riskier behaviour, such as venturing further from shelter[17]. These behavioural changes cause increased mortality from predation in mesocosm and patch-reef experiments[16–19]. Although these studies suggest that higher CO_2 levels could reduce the replenishment rate of reef fish populations, there is also variation among species in their sensitivity to elevated CO_2 (ref. 18). Consequently, some reef fish species are expected to be more affected than others. A major limitation in making predictions about the effects of behavioural alterations in marine fish is lack of knowledge of the impacts of higher CO_2 levels in natural communities. Whether reef fish behaviours acclimate to high CO_2 when individuals are continuously exposed to high CO_2 in their natural environment, and the potential consequences of altered behaviour on community structure, are unknown. There may also be energetic costs to living in a high-CO_2 environment[20]. Increased ion exchange required to offset the acidifying effects of higher CO_2 levels on blood and tissue pH could incur greater energetic demands on the fish[5,21,22], potentially leading to less energy available for other essential activities, or reducing the scope for aerobic performance[20,23].

We used natural CO_2 seeps in Papua New Guinea[24] to test the effects of continuous exposure to elevated CO_2 on reef fish behaviour and metabolism in their natural habitat, and to examine the potential consequences for reef fish communities. At these sites, fish communities occupy reefs near cool volcanic seeps that acidify seawater to levels similar to projections for the coming century (median pH (total scale) 7.72–7.95, pCO_2 441–998 μatm; Supplementary Table 1). Nearby reefs unaffected by the CO_2 seeps are ideal controls (pH 7.98–8.02, pCO_2 346–413 μatm; Supplementary Table 1). We first tested the behaviour of juveniles from two damselfish species (*Dascyllus aruanus* and *Pomacentrus moluccensis*) and two cardinalfishes (*Apogon cyanosoma* and *Cheilodipterus quinquelineatus*) at two sites, Upa Upasina and Dobu (Supplementary Information). Resting and maximum oxygen consumption rates were determined for the two damselfish species to assess metabolic performance. Experiments were conducted aboard a ship moored near the seeps. By selecting highly sedentary fishes with small home ranges, we were able to test behaviour and metabolism in juvenile fish that have experienced acidified conditions since recruitment to the reef habitat at the end of their larval phase. We then compared the structure of fish communities between CO_2 seeps and control reefs at three locations: Upa Upasina, Dobu and Esa'Ala. Because a previous study at the same location[24] investigated the effects of elevated CO_2 and acidification on the coral community, it was also possible to consider how changes in the coral community caused by higher CO_2 levels could affect the structure of fish communities.

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All four species of fish from the CO_2 seep exhibited strikingly different behaviours compared with fish from the control reef ($p < 0.001$ for all comparisons). As expected, fish from the control reef strongly avoided a water stream containing odour from a predator (the rockcod, *Cephalopholis cyanostigma*) in a two-channel flume, spending all of their time in the water stream without predator odour (Fig. 1a). In contrast, fish from the CO_2 seep exhibited a strong attraction to predator odour, spending over 90% of their time in the water stream containing predator odour (Fig. 1a). The results were similar among the four species. Fish from the control reef were also able to distinguish between water from the control reef and water from the CO_2 seep, strongly preferring the water from the control reef (Fig. 1b). In contrast, fish from the CO_2 seep spent approximately equal amounts of time in the two water streams (Fig. 1b). Control fish retained their preference for control reef water, even when water from the CO_2 seep had been aerated to restore pH and pCO_2 to control levels (Supplementary Fig. 1), indicating that the control fish preferred the odour or other chemical properties of water from the control reef and were not simply avoiding the high pCO_2. When tested with offshore water that had been conditioned with benthic communities from the CO_2 seeps (PVC plates deployed underwater for 14 months) versus offshore water conditioned with benthic communities from control reefs, control fish strongly preferred the water stream conditioned with benthic communities from the control reef (Fig. 1c). As observed in the previous trial, high-CO_2 fish spent approximately equal amounts of time in the two water streams (Fig. 1c).

Fish from the CO_2 seep also exhibited very different levels of activity and boldness. For all four species, fish from the control reef spent ≥ 80% of their time in shelter. In contrast, the two damselfishes from the CO_2 seeps spent less than 12% of their time in the shelter and the two cardinalfishes from the CO_2 seep did not use the shelter at all (Fig. 2a; CO_2 treatment $p < 0.001$). Fish from the CO_2 seep ventured further from shelter compared with fish from the control reefs, and the pattern was similar among species (Fig. 2b; CO_2 treatment $p < 0.001$), except that all cardinalfishes ventured the maximum distance possible (far end of the tank), whereas not all damselfishes ventured the maximum distance. Activity levels differed both between species and CO_2 level (CO_2 treatment*species interaction $p < 0.001$). For the two damselfishes, fish from the CO_2 seep were less active than fish from control reefs. These fish remained relatively inactive in a position well away from the shelter, whereas fish from the control reef were more active but remained near the shelter. For the two cardinalfishes, individuals from the CO_2 seep were nearly an order of magnitude more active than fish from the control reef, swimming continuously around the tank, whereas control fish mostly sheltered in the hide (Fig. 2c). The large difference in activity level between CO_2 seep and control cardinalfishes is consistent with previous studies indicating that these fishes may be especially sensitive to elevated CO_2 (ref. 23). Finally, fish from the CO_2 seep were much bolder than fish from control reefs, emerging from shelter at least six times faster after disturbance (Fig. 2d; CO_2 treatment $p < 0.001$).

There were no differences in resting or maximum oxygen consumption between fish from the CO_2 seeps and control reefs for the two damselfishes, *P. moluccensis* and *D. aruanus* ($p > 0.35$ for all comparisons; Supplementary Fig. 2). Metabolism was not tested for the two cardinalfishes.

Despite the pronounced effects of high CO_2 on fish behaviour, there were relatively few differences in species richness, species composition and relative abundances of fish between the CO_2 seep and control reefs. Average species richness on timed swims at the three CO_2 seeps (129.3 ± 9.9 s.e.m. species) did not differ from species richness at three comparable control sites (138.3 ± 4.5 species). Similarly, there was no significant difference in species richness of transect counts at Upa Upasina (49.2 ± 3.7 species per transect at the CO_2 seep versus 52.7 ± 1.7 species per transect at the control reef).

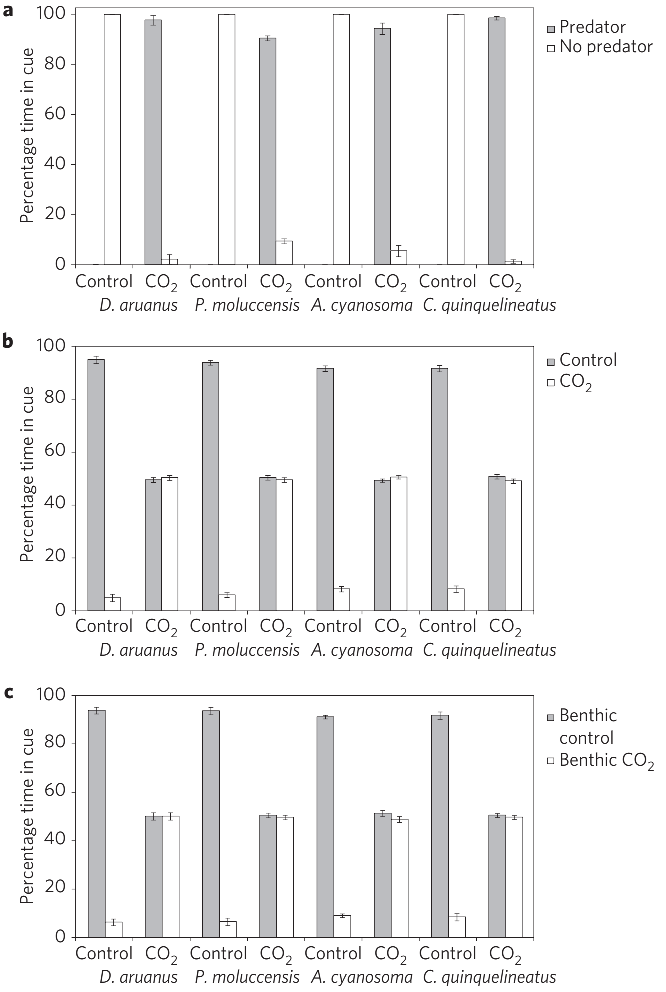

Figure 1 | Preference of juvenile fish for water streams containing different chemical cues presented in a two-channel flume chamber. Juvenile fish from either the control or CO_2 reef were given the choice of: offshore water with or without predator odour (**a**), water from the CO_2 seep site or the control reef (**b**), offshore water conditioned with chemical cues of benthic communities from the CO_2 seep or the control reef (**c**). Graphs show the mean percentage time (± s.e.m.) spent in each water stream. For each cue combination (A, B, C) a total of 20 fish from each species were tested (10 control and 10 CO_2 seep), except for *P. moluccensis*, where a total of 40 fish were tested for each cue combination (20 control and 20 CO_2 seep).

There was no difference in fish community structure between the CO_2 seep and control reef at Dobu and Esa'Ala (Fig. 3a). The fish community at Upa Upasina was different from the other two locations (similarity profile (SIMPROF) test, $p = 0.001$) and there was also significant segregation of community structure between the CO_2 seep and control reefs at this location (SIMPROF test, $p = 0.028$; Fig. 3a). However, the difference between the CO_2 seep and control reef at Upa Upasina was much smaller than the differences between these two reefs and the other two locations. Counts of fish species along transects at Upa Upasina further supported the significant differences in fish community structure at the CO_2 seep, with a significant difference in community structure of fishes on transects within the CO_2 seep compared with the adjacent control reef (Fig. 3b; analysis of similarities (ANOSIM) Global $R = 0.93, p = 0.029$). The difference between fish communities at the CO_2 seep and control reefs at Upa Upasina was mostly driven by small bodied species

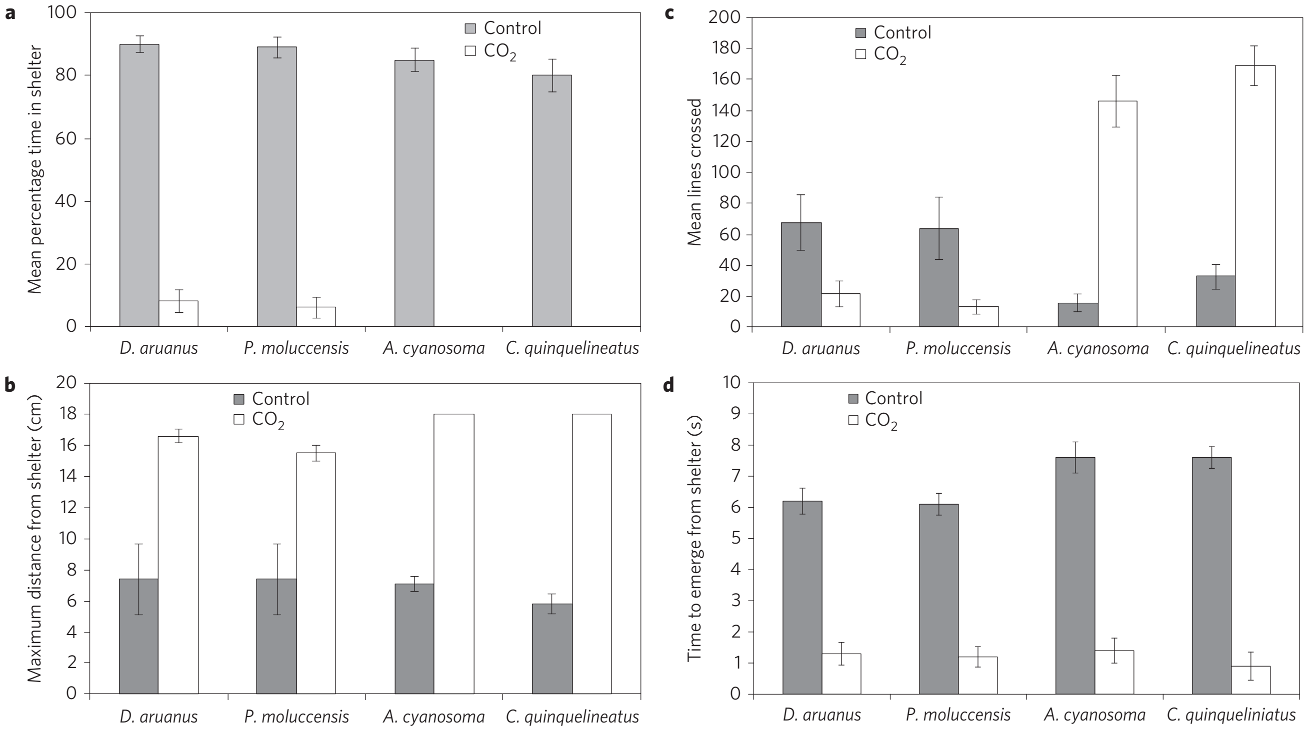

Figure 2 | Activity level and boldness of fish from CO_2 seep and control reefs. **a**, Percentage of time (± s.e.m.) in shelter. **b**, Maximum distance from shelter. **c**, Activity level estimated as the number of lines crossed during the observation period (5 min). **d**, Time taken to emerge from shelter after disturbance. Behaviour was measured for juvenile fish in an aquarium containing a small colony of the coral *Pocillopora damicornis*. For each species a total of 20 fish were tested (10 control and 10 CO_2 seep).

that are very habitat dependent. The 15 species that contributed most to dissimilarities between CO_2 and control locations came from five families, with average maximum lengths < 10 cm in four of these families (Fig. 3c). The five species that contributed most to community dissimilarities (a combined total of 17.3%) were all more abundant at the CO_2 seep (Fig. 3c). Most of the other species were more abundant at the control reef, although with the exception of *P. moluccensis*, all were relatively uncommon.

Our results show that juvenile fish living at the CO_2 seeps exhibited almost identical sensory impairment and behavioural abnormalities to juvenile fish reared at similar CO_2 levels in the laboratory. Age estimates from otoliths indicate that the juvenile fish had been on the reef for three to five weeks on average (Supplementary Information). Because these small fish are highly sedentary, with home ranges of just a few square metres, this demonstrates that behaviour does not acclimate to elevated CO_2 with continuous exposure in natural habitat. Furthermore, because most mortality of juvenile fish occurs within the first few days of settlement to the reef[25], these fish would have already been exposed to any post-settlement selection favouring CO_2 tolerance. Nevertheless, they were still behaviourally impaired. There was no apparent increase in the energetic cost of living at the CO_2 seep, with similar rates of resting and maximum oxygen consumption to fish from the control reef. This is also consistent with laboratory studies that have found either no effect, or even positive effects, of similar CO_2 levels on damselfish oxygen consumption rates[26]. Consequently, it appears that reef fish exposed permanently to near-future ocean acidification suffer serious behavioural changes, but their physiological performance is not compromised. The effects of high CO_2 on behaviour are probably due to interference with neurotransmitter receptor functions caused by sustained changes in acid–base relevant ion concentrations in the blood and tissue of the fish at high CO_2 (refs 3,16).

Experimental studies conducted in coral reef habitat demonstrate that CO_2-induced behavioural changes, similar to those observed here in fish from the CO_2 seeps, increases mortality from predation by over fivefold in newly settled fish[16–18]. Even when predators are also exposed to the same high CO_2 as their prey, mortality rates of small damselfishes are double those of controls[19]. Despite the impaired behaviour of juvenile fish in the CO_2 seeps, which is likely to increase their predation risk, the structure of the fish community differed relatively little between CO_2 seeps and control reefs. Owing to the small spatial extent of the seeps ($< 5{,}000\ \mathrm{m}^2$) it is possible that there is currently sufficient recruitment of larval fish from surrounding healthy reefs to offset any increased mortality within the seeps caused by the behavioural changes. Larval fish recruit in high abundance[25] and density-dependent mortality may buffer adult numbers from variation in juvenile mortality[27]. As a result, a higher predation rate of small juveniles at the CO_2 seep might not directly affect adult population size. Our surveys of fish community structure included large juvenile and adult fishes, but not the small juveniles that are most susceptible to predation[25]. Furthermore, the number of large predatory fishes that could prey on recruits and small juveniles (Supplementary Table 2) was lower at the CO_2 seep (average of 16.2 predators per transect) compared with the control reef (average of 26 predators per transect, $p = 0.025$). Large predatory reef fishes prefer complex reef habitats with branching and table *Acropora* corals[28], not massive corals, which may explain their higher abundance at the control reef, although there could potentially be direct effects of elevated CO_2 on the predators. A lower abundance of predators at the seep could offset the increased risk of mortality due to abnormal behaviour.

The higher abundance of five small fish species in the CO_2 seep at Upa Upasina could be due to the greater abundance of massive *Porites* corals than at control reefs, and the many caves and large holes produced by CO_2 erosion[24]. The two planktivorous

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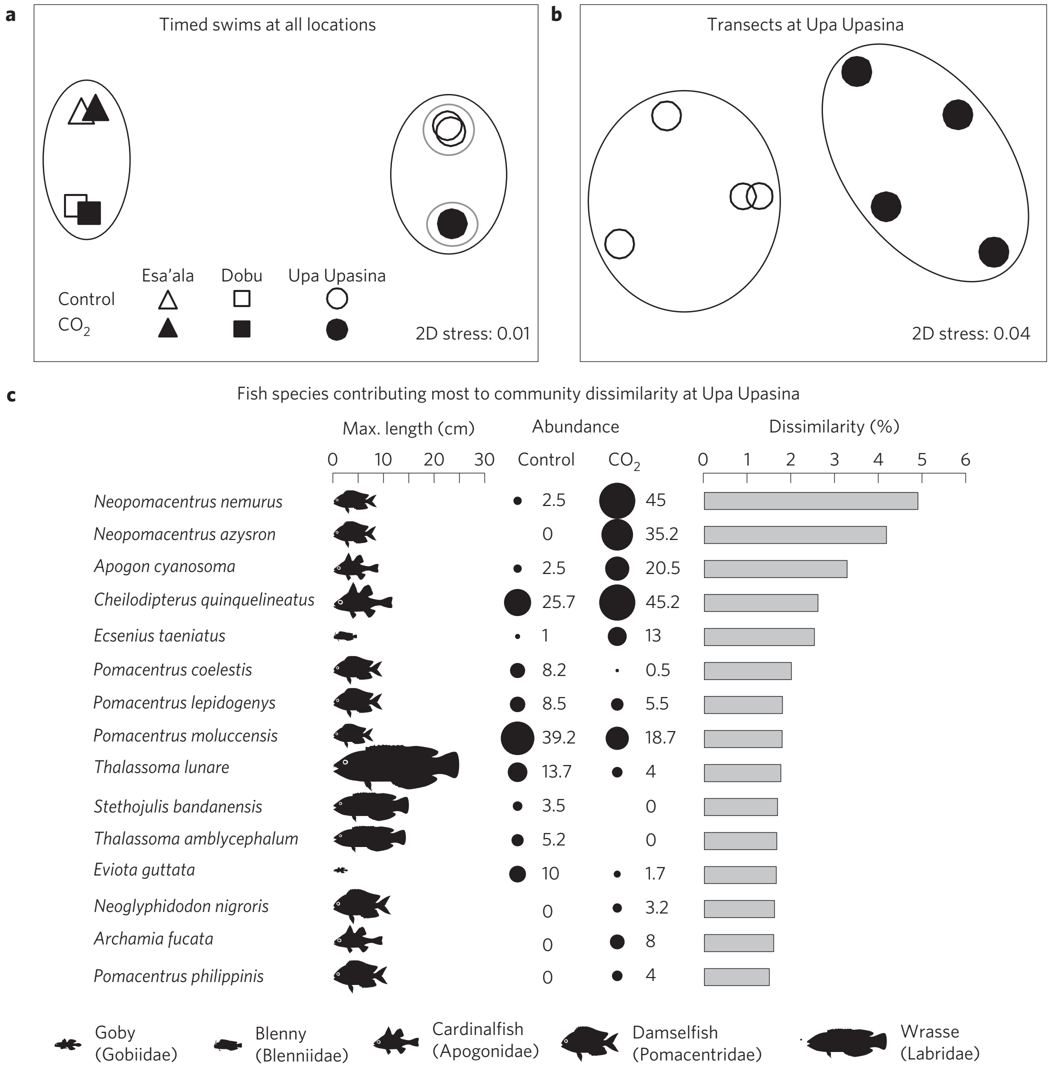

Figure 3 | Comparisons of fish community structure at CO_2 seep and control locations. **a**, nMDS plot using ranked species abundance data from timed swims. Black and grey ellipses separate communities that differed significantly (SIMPROF test, $p=0.001$ and $p=0.028$ respectively). **b**, nMDS plot using abundance data from transects at Upa Upasina. Black ellipses separate communities that differed significantly (ANOSIM Global $R=0.927, p=0.029$). **c**, Fish species that made the greatest contribution to the average community dissimilarity between CO_2 seep and control locations based on SIMPER analysis. The maximum length of each species is indicated by a fish silhouette and relative abundances are shown as bubbles of proportionate size. Mean abundance per transect is presented alongside. The percentage contribution of each species to average community dissimilarity is shown by the grey horizontal bar.

damselfishes, two cardinalfishes and one blenny prefer elevated positions around massive corals for feeding and/or caves in which to shelter. We hypothesize that habitat changes at the CO_2 seep favour these particular species. Conversely, the higher abundance of the damselfish *P. moluccensis* at the control reef could be explained by the higher abundance of its preferred branching coral habitat at the control reef. Consequently, the few clear differences in fish community structure could be driven by the differences in habitat composition and structure at the CO_2 seep, not by the direct effects of high CO_2.

Although our results indicate that fish communities at CO_2 seeps are not strongly affected by the behavioural effects of high CO_2, they may be impacted in the future, as all reefs become acidified as a result of continued uptake of anthropogenic CO_2 from the atmosphere. As acidification becomes widespread there will no longer be the potential for demographic subsidy of larvae or adults from nearby unaffected reefs. Instead, behavioural abnormalities in fish on all reefs is likely to depress the rate of recruitment and population replenishment on a broad scale. Importantly, our results show that the behavioural abnormalities observed in juveniles are not ameliorated by continued exposure to elevated CO_2. Although an initial study suggests that parental exposure to high CO_2 can partially reduce the effects of high CO_2 on some locomotory traits important to escaping predators (for example, escape speed and duration)[29], it does not restore performance in other traits (for example, escape trajectory)[29]. Consequently, if reef fish behaviour does not adapt to rising CO_2 levels over coming generations, there could be serious consequences for the structure and function of future reef communities.

Methods

Behavioural trials. Olfactory preferences were tested in a two-channel choice flume[1]. Two different water streams were gravity fed into the flume at 100 ml min^{-1} using flow controllers. Fish were released at the downstream end of the flume, where they were free to move to either side or swim towards the preferred water source. The choice of each fish for the two water streams was tested for a total of 4 min, with the side of the water sources swapped after 2 min

(Supplementary Information). Three different cue combinations were tested: offshore water conditioned with predator odour versus offshore water without predator odour, water from the CO_2 seep site versus water from the control reef, offshore water conditioned with chemical cues of benthic communities from the CO_2 seep versus chemical cues of benthic communities from the control reef (see Supplementary information for details of cue preparation). Ten individuals of each fish species from the CO_2 seep and from the control reef were tested for each cue combination. Juvenile fish were collected from CO_2 seep and control reefs using small hand nets and tested within 12 h of capture. Kolmogorov–Smirnov tests were used to compare the proportion of time that individuals from the CO_2 seep and control reef spent on the side of the chamber containing the focal cue.

Activity and boldness were tested by placing a single fish in an aquarium with a small colony of the coral *Pocillopora damicornis* on one side of the tank for shelter. The front of the tank was marked with grid-lines at 3 cm intervals so that movement could be quantified, and the other sides of the tank were covered with black plastic so the fish could not see other stimuli. The observer remained still while recording observations. After 2 h habituation time each fish was observed for 5 min, recording: the number of lines crossed, as a proxy for activity level; the maximum distance moved from the habitat; the total distance moved; and the amount of time the fish spent in the coral shelter. At the conclusion of the 5 min observation period fish were chased into the coral using a pencil and the amount of time it took for the fish to re-emerge from the shelter was recorded. All observations were conducted between 14:00 and 18:00 for the diurnally active damselfishes and between 20:00 and 00:00 for the nocturnally active cardinalfishes. Two-way analysis of variance (ANOVA) was used to determine whether the behaviour of fish differed significantly between the site where they were collected (CO_2 seep or control) and between species, as well any interaction between these two factors.

Respirometry. The maximum rate of oxygen consumption ($MO_{2\mathrm{Max}}$) in fish was measured following the standard chase method[30]. An individual fish was placed in a 0.4 m (diameter) container filled with ambient seawater and chased continuously by hand for 3 min in a figure-eight motion, not allowing the fish to slow down or stop. The fish was then scooped into a mesh net and maintained out of the water for 1 min, after which it was immediately placed in a 1,615 ml closed-loop recirculating respirometry chamber, submerged in a water bath supplied with ambient seawater. Oxygen measurements commenced within 10 s of placing the fish in the chamber and continued for 5–7 min. The value of $MO_{2\mathrm{Max}}$ (mg O_2 kg^{-1} h^{-1}) was calculated from the steepest slope of decline in oxygen concentration in the chamber (at least 60 s in duration). To obtain resting or standard metabolic rates, fish were left in the intermittent-flow respirometry chambers for an additional 6–8 h until oxygen consumption rates stabilized ($MO_{2\mathrm{Rest}}$). A submersible pump flushed the chamber with clean, well-oxygenated seawater on a 15 min on/10 min off cycle, while a recirculating in-line pump ensured that water within the chamber was thoroughly mixed during the entire trial. Oxygen concentration during the 'off' phase remained above 80% air saturation. The value of $MO_{2\mathrm{Rest}}$ was calculated from the average of the lowest 10% of MO_2 values over the 6–8 h recovery period (see Supplementary Information for further details). Aerobic scope was calculated as the difference between $MO_{2\mathrm{Rest}}$ and $MO_{2\mathrm{Rest}}$. Paired t-tests were used to compare $MO_{2\mathrm{Rest}}$, $MO_{2\mathrm{Max}}$ and aerobic scope between control and high-CO_2 fish for each species using SigmaPlot (Systat Software).

Fish diversity and community structure. Fish species richness and relative abundance were surveyed at Upa Upasina, Esa'Ala and Dobu. At each location, all species present and their abundance on a log 5 scale were recorded along a 40 m × 10 m transect at approximately 3 m depth within the CO_2 seep site and nearby control sites (one control site at Esa'Ala and Dobu and two control sites at Upa Upasina). Each transect was surveyed for a total of 45 min by two divers. We made log 5 counts rather than more time consuming absolute counts owing to limited time at Esa'ala and Dobu. At Upa Upasina we also quantified the absolute abundance of all fish species present on four replicate 30 m transects each within the CO_2 seep and the main control site. Transect width was 2 m for small sedentary species and 10 m for large mobile species.

Non-metric multi-dimensional scaling (nMDS) based on the Bray–Curtis similarity measure was used to investigate patterns in community structure among seep and control locations using ranked data from log 5 counts of species. A similarity profile (SIMPROF) tested for statistical significance of clusters in these data. nMDS was also used to investigate differences in fish community structure among the replicate transects at Upa Upasina. In this case, species abundance data were square root transformed before analyses, to down-weight the influence of very abundant species. Differences between the seep and control groups were estimated using analysis of similarities (ANOSIM). The contribution of each species to the average dissimilarity between seep and control groups was estimated using similarity percentage analysis (SIMPER). All multivariate analyses were performed using Primer (Version 6.1.12, Plymouth Marine Laboratories). A one-tailed t-test was used to test if the average abundance per transect of large predatory fishes at Upa Upasina was lower at the CO_2 seep compared with the control reef.

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Author contributions

All authors contributed to the designs of the study, collection and analysis of data, and writing the article.

Additional information

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Competing financial interests

The authors declare no competing financial interests.