Ocean acidification alters fish–jellyfish symbiosis

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Symbiotic relationships are common in nature, and are important for individual fitness and sustaining species populations. Global change is rapidly altering environmental conditions, but, with the exception of coral–microalgal interactions, we know little of how this will affect symbiotic relationships. We here test how the effects of ocean acidification, from rising anthropogenic CO2 emissions, may alter symbiotic interactions between juvenile fish and their jellyfish hosts. Fishes treated with elevated seawater CO2 concentrations, as forecast for the end of the century on a business-as-usual greenhouse gas emission scenario, were negatively affected in their behaviour. The total time that fish (yellowtail scad) spent close to their jellyfish host in a choice arena where they could see and smell their host was approximately three times shorter under future compared with ambient CO2 conditions. Likewise, the mean number of attempts to associate with jellyfish was almost three times lower in CO2-treated compared with control fish, while only 63% (high CO2) versus 86% (control) of all individuals tested initiated an association at all. By contrast, none of three fish species tested were attracted solely to jellyfish olfactory cues under present-day CO2 conditions, suggesting that the altered fish–jellyfish association is not driven by negative effects of ocean acidification on olfaction. Because shelter is not widely available in the open water column and larvae of many (and often commercially important) pelagic species associate with jellyfish for protection against predators, modification of the fish–jellyfish symbiosis might lead to higher mortality and alter species population dynamics, and potentially have flow-on effects for their fisheries.

1. Introduction

Symbiotic relationships are ubiquitous in the terrestrial and marine realms and sustain species diversity and various important ecological processes [1,2]. For positive symbiotic interactions, such as mutualism or commensalism, at least one of the species involved benefits from the interaction. Such interactions are important because they mediate the persistence of other species through facilitation, particularly in conditions of high disturbance, stress or predation [3]. Mutualism and commensalism provide benefits in terms of resources, such as food, habitat and shelter, and such positive interactions are important drivers of species population dynamics, species distributions and diversity, and community organization [4].

Perhaps due to the vastness of the ocean, symbiotic relationships in the sea—other than coral–zooxanthellae symbiosis—are less well studied and understood than on land [5]. However, they occur globally in tropical, temperate and polar regions, and cover a wide range of benthic and pelagic species [6]. A well-known marine symbiosis is that between anemones and clown-fishes (e.g. [7]), popularized through the animated movie Finding Nemo. However, fishes also form symbiotic relationships with other taxa such as jellyfish, the pelagic relatives of anemones. Fish–jellyfish interactions are complex as they include predation by jellyfish on larval fish, predation by fishes on jellyfish, competition for...
Jellyfish frequently form very dense blooms, predominantly during spring and summer [13], which often coincides with the timing of the pelagic larval phase of fish species [14]. Many of the fishes that associate with jellyfish are commercially important, including pollock, jacks and trevallies [9,15]. By hosting these species during their early life-history stages, jellyfish may thus benefit commercial fisheries. However, there is a gap in our understanding of how climate stressors might affect mutualistic or commensal relationships in general [16], and fish–jellyfish associations in particular. Ocean warming and acidification resulting from increasing anthropogenic CO2 emissions alter a wide array of critical behaviours in marine vertebrates and invertebrates [17,18], but, with the exception of coral–zooxanthellae relationships, their effects on symbioses have not been established. Here we test whether ocean acidification can alter the symbiotic association between juvenile fish and their jellyfish host through visual as well as olfactory sensory modalities, as these senses are known to be affected by high CO2. We show that fishes are not attracted to jellyfish olfactory cues, but that ocean acidification reduces the combined visual/olfactory attraction of fishes towards their host jellyfish, causing them to spend more time away from the jellyfish’s protective umbrella and oral arms. Such altered interactions that increase predation risk may have consequences for early-life survival of pelagic species.

2. Material and methods

(a) Study area and species

We studied the effects of ocean acidification on interactions between the blue blubber jellyfish *Catostylus mosaicus* (Scyphozoa; Rhizostomeae) and three species of fish. *Catostylus mosaicus* is a large medusa (maximum bell diameter approx. 35 cm) that forms conspicuous blooms in estuaries and coastal waters of eastern Australia. During blooms, densities of adult jellyfish can exceed 1 m$^{-3}$ [19] and peak densities of small medusae can attain 100 m$^{-3}$ [20]. The three species of fish were selected for their variety of responses to jellyfish. Juveniles of the yellowtail scad (*Trachurus novaezelandiae*) frequently associate with *C. mosaicus* [9], and the species was selected to determine whether exposure to CO2 affected the ability of fish to interact with the jellyfish. Mulloway (*Argyrosomus japonicus*) do not associate with jellyfish, and barramundi (*Lates calcarifer*) actively avoid water containing the olfactory cues of jellyfish [21]. These last two species were selected to determine whether their ability to recognize olfactory cues of jellyfish would be affected by elevated CO2.

To assess the prevalence of jellyfish–fish associations, during a jellyfish bloom event we counted the number of fish associated with 62 *C. mosaicus* in southern Moreton Bay, Queensland (17 October 2014). Jellyfish and their associated fish were captured using a dip net (70 cm diameter, 1 mm mesh). Jellyfish were removed from the net and their bell diameter was measured prior to them being released. The average bell diameter of the jellyfish sampled was 17.9 ± 1.8 cm (s.d.), with a range of 12.5–24.0 cm. During the field collections, only *T. novaezelandiae* were found associated with the jellyfish. All fish captured with the jellyfish were transferred to a polystyrene container of seawater that was aerated continuously during transport to the laboratory and used for subsequent vision and olfaction experiments.

(b) CO2 manipulation of yellowtail scad

After capture from the field, fishes were directly transferred to a constant-temperature room set at 24°C at Griffith University. Fishes were randomly allocated to each of four 60 l plastic bins filled with seawater (salinity 36 units) collected from the Gold Coast Seaway on rising tide and passed through a sand filter. The fishes were acclimated in ambient seawater (i.e. ‘high pH’ and ‘low pCO2’, representing present-day conditions) in their respective bins for approximately 9 days before the CO2 treatment (i.e. ‘low pH’ and ‘high pCO2’, representing future conditions) started. Two bins were allocated to each of two pH treatments: approximately 7.9 (present day) and approximately 7.6 (future scenario; table 1). The low-pH treatment was based on the RCP 8.5 emission scenario (business-as-usual scenario) with a predicted mean (± s.d.) decrease in ocean surface pH of approximately 0.33 ± 0.003 units by 2100 compared with the 1990s [22]. The two bins of each treatment shared a 200 l header tank. In the low-pH treatment, CO2 was gradually elevated in the header tank from ambient to future conditions over a period of 2 days. pH was manipulated by bubbling pure CO2 into a 101 bucket, after which the enriched water was mixed (with a 2001 h$^{-1}$ pump) with that in the low-pH header tank until the desired pH$_{NBS}$ of 7.6 was attained, as measured with a Mettler Toledo Five Go 2. During this mixing process, the outflow from the header tank to the fish holding bins was interrupted for a few minutes. Addition of CO2-enriched water to the low-pH header tank was done twice daily (9.00 and

<table>
<thead>
<tr>
<th>treatment</th>
<th>$T$ ($^\circ$C)</th>
<th>pH$_{\text{NBS}}$</th>
<th>salinity</th>
<th>$n$</th>
<th>TA (mmol kg$\text{SW}^{-1}$)</th>
<th>pCO$_2$ ($\mu$atm)</th>
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<td>7.95 (0.01)</td>
<td>35.0 (0.0)</td>
<td>14</td>
<td>2331 (7)</td>
<td>740 (29)</td>
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<tr>
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<td>7.61 (0.01)</td>
<td>35.0 (0.0)</td>
<td>14</td>
<td>2369 (6)</td>
<td>1794 (31)</td>
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<td>scad</td>
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<td>26.3 (0.1)</td>
<td>8.07 (0.01)</td>
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<td>673 (10)</td>
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<td>38.6 (0.1)</td>
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<td>2521 (15)</td>
<td>1464 (31)</td>
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<td>8.02 (0.01)</td>
<td>38.3 (0.1)</td>
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<td>734 (15)</td>
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Excess food and debris was removed from tanks each morning.

Office water exceeded 80% throughout the experiment. Fish were fed OptiOx that was calibrated daily. Oxygen saturation of the water exceeded 80% throughout the experiment. Fish were fed daily with live Artemia as well as dried commercial fish feed. Excess food and debris was removed from tanks each morning.

(c) CO₂ manipulation/larval rearing of barramundi and mulloway

Fertilized mulloway and barramundi eggs were obtained from the South Australian Research and Development Institute (first-generation broodstock) and from a commercial hatchery (Robarza, seventh-generation broodstock), respectively. Both species were reared simultaneously (in separate tanks) at the University of Adelaide under current and future CO₂ levels (table 1). Larvae were exposed to their respective treatments until they had undergone metamorphosis and approached their settlement stage, which was 24–25 days post-hatching (dph) for mulloway and 19–20 dph for barramundi. For each species and each of their two CO₂ treatments, larvae were reared in four replicate 60 l food-safe rearing tanks. Seawater was sourced from Gulf St Vincent (approx. 10 m depth, several kilometres offshore) and recirculated in a closed system, with each rearing tank connected to its own 20 l sump containing a biological filter, a protein skimmer (WG-308, Boyu, China) and a UV sterilizer (UView, Blue Planet, China).

(d) Analysis of carbonate chemistry

The CO₂ partial pressure in the seawater was calculated for all three fish species using measured values of temperature, salinity, pHNBS and total alkalinity (TA) in the fish holding tanks (table 1), using the software CO2SYS [24] with constants K1 and K2 from Mehrbach et al. [25] and refit by Dickson & Millero [26]. Fewer salinity measurements in the fish holding tanks were gravity-fed into the respective fish holding bins at a rate of approximately 120 ml min⁻¹ (approx. 173 l per day).

(e) Combined visual/olfactory choice tests

The association between juvenile yellowtail scad and jellyfish was tested at Griffith University in a glass aquarium. An aquatorium of 50 × 20 × 40 cm (L × W × H) was filled with either ambient or CO₂-treated water, of similar values as those in the fish holding tanks to avoid measuring potential shock effects in the fish due to transfer to water of different chemistry. The jellyfish were not pre-adapted to the high-CO₂ water, but observations did not reveal distinct differences in the (tethered) jellyfish behaviour between choice arenas for the different treatments. The water in the choice tank was also of the same temperature as that of the fish holding tanks (24 °C). One of two medusae (bell diameter 16.5 and 17.5 cm, respectively) was tethered in the top corner of the tank using a thin rope that was fixed loosely around the peduncle of the bell (electronic supplementary material, figure S1). If the jellyfish did not pulsate actively during the experiment, then it was replaced with another jellyfish. A single fish (approx. 5 cm total length) was introduced to the opposite lower corner of the tank using a vertical tube and its movements recorded from the side using a camcorder (HF R406 Legria, Canon, Japan) during 10 min. The seawater in the choice tank was replaced with fresh water (either of ambient or high CO₂, depending on the treatment being tested) for every second fish. Each fish was used only once and the number of replicates per treatment is reported in figure 2.

(f) Olfactory choice tests

Olfactory response to jellyfish chemical cues was tested for yellowtail scad at Griffith University, and for barramundi and mulloway at the University of Adelaide. All fish tested were approximately 1 cm in total length. Control yellowtail scad were deterred by jellyfish olfactory cues (see Results) and therefore olfactory cues were not considered as an important driver of the fish–jellyfish associations. Owing to relatively low numbers of yellowtail scad caught and animal ethics considerations we used the remainder of the fish to perform the combined visual/olfactory choice test (representative of what the fish would experience in situ) in which we did observe a high-CO₂ effect on the fishes.

All jellyfish used for the trials were collected from Moreton Bay, Queensland. For trials at Griffith University, jellyfish were collected the day before the trials and maintained in 50 l tanks. For trials at the University of Adelaide, four blue blubber jellyfish C. mosaicus were directly flown to Adelaide where they were maintained in a 150 l aquarium and fed Artemia nauplii daily. Jellyfish olfactory cues were prepared immediately before each choice test by immersing one jellyfish in fresh seawater in a 20 l bucket for 1 h. The jellyfish cue water was then filtered through a 10 μm filter bag to remove sting cells.

The responses of the three fish species to jellyfish olfactory cues were tested using a two-channel choice-flume (13 × 4 cm), developed by Gerlach et al. [27]. The flume allows pairwise choice experiments in which individual fish can move freely between water originating from two different sources that continuously flows from one end to the other end of the flume. Dye tests were conducted at least once per day to ensure distinct and parallel water flows in each flume channel, without any turbulence or eddies. Dixson et al. [28] observed that using either acidified or control water in flume choice tests did not affect behavioural choices and thus water of ambient pH was used throughout all olfactory choice trials. For each trial, water from the two different treatments (control and jellyfish olfactory cues) was gravity-fed from buckets into the choice-flume at a rate of approximately 100 ml min⁻¹. The water in the buckets was of the same temperature as that of the fish holding tanks. Trials were performed following Dixson et al. [28], where an individual fish was placed at the downstream end of the flume and left to acclimate for 2 min while exposed to both water flows with different cues and able to explore both sides of the flume. After acclimation, the position of the fish was...
video-recorded for 2–2.5 min (depending on the species). This was followed by a 1 min rest period during which the water cue sides were switched (controlling for any side preferences) after which the entire process including acclimation was repeated. The fish movements during the trials were recorded from above using a camcorder (HF R406 Legria, Canon, Japan) to avoid any observer’s effects. Each fish was used only once and the number of replicates per treatment is reported in figure 2.

(g) Analysis of fish behaviour
For the olfactory choice tests, the location of the head of the fish (left versus right flume channel) was visually determined from the video recordings every 5 s for the period before as well as after the side switch in cue water. Fish that did not explore both channels of the chamber during the acclimation period were not included in the analysis as these were not deemed to have assessed the choices available (n = 1 control yellowtail scad; n = 1 high-CO2 mulloway).

For the combined visual/olfactory choice test, the position of the fish in the choice chamber was continuously and automatically tracked from the 10 min video recordings using ETROVISION XT10 (Noldus Information Technology, Wageningen, The Netherlands). The combined use of remote recordings and automated tracking eliminated the risk of observer bias and external influences on behaviour caused by the presence of the observer. ETROVISION calculated the amount of time the fish spent in the ‘jellyfish zone’ and the number of times the fish approached the jellyfish (i.e. entered the jellyfish zone from zone 2). The jellyfish zone was defined as a rectangle (side view, electronic supplementary material, figure S1), with the width defined as the distance between the tank wall and the most distal part of the bell when the jellyfish tether was stretched maximally, and height as the distance between the water surface and the lowest point of the arms when the jellyfish tether was stretched maximally. Three other zones, located at increasing distances from the jellyfish, were also included (electronic supplementary material, figure S1), and all four zones were of equal volume.

(h) Statistical analyses
For each of the two CO2 treatments, percentage of time spent at the flume side with jellyfish olfactory cues was compared to a random 50% distribution (i.e. equal distribution at both sides in case there was no response to the cue) using either a one-sample t-test or a Wilcoxon signed-rank test, depending on whether the data were normally distributed as tested with a Kolmogorov–Smirnov test of normality.

For the combined visual/olfactory choice experiment, total time spent in each of the four zones of the choice arena was compared between fish from the ambient and elevated CO2 treatments using an independent-samples t-test on log-transformed data. In cases where variances were not homogeneous, the output of an adjusted t-test was used, based on lower degrees of freedom (automatically calculated within IBM SPSS v. 20). The same statistical analysis was used to test for the number of fish transitions from zone 2 to the jellyfish zone. Percentage of time spent in the jellyfish zone and number of jellyfish approaches represent different behavioural traits because a fish could, for example, approach the jellyfish once and remain associated with it for an extended period, or approach it multiple times but associate only for a short period, both of which scenarios could lead to a similar total time spent in the jellyfish zone.

In addition, the percentage of all individuals from each treatment that entered the jellyfish zone was calculated and tested with a binomial test. Because the four zones were not located at equal distances from one another and because the fish were not released at an equal distance from each zone (electronic supplementary material, figure S1), there was no a priori expectation of the chance of a fish occupying a zone (e.g. 25 : 25 : 25 : 25% in case of a fish being released in the centre of an aquarium at the position where all four zones intersect when they are located at equal distances from one another). Therefore, we simply tested against a 0.5 probability based on a behavioural outcome of either willing or unwilling to associate with the jellyfish.

3. Results
Fish–jellyfish associations (figure 1) were observed in the field for 32% of the 62 jellyfish sampled. Jellyfish harboured 0–3 fish with a mean density of 0.5 ± 0.7 (s.d.) fish per jellyfish. All associated fish were juvenile (size range approx. 1–5 cm total length, with 89% less than 2.5 cm) yellowtail scad (Trachurus novaezelandiae). There was no relationship between jellyfish bell size and number of associated fishes (linear regression: R² = 0.00, p = 0.975).

Total time spent close to jellyfish in the choice arena was approximately three times shorter (t-test, t31 = −2.364, p = 0.025) for fish from the high-CO2 treatment compared with the control treatment (figure 2a). Although fish in the high-CO2 and control treatments only spent 2.6 ± 1.4% and 8.0 ± 2.2%, respectively, of the total observation time in the jellyfish zone, this difference was still significant (t31 = −2.170, p = 0.038) when standardized to total observation time. Time spent in the other zones of the choice arena did not differ between the two treatments (adjusted t-test, t26.4 ≥ 1.347, p > 0.189). Nevertheless, there was a trend of a higher percentage of time spent in the zone near the jellyfish by the high-CO2-treated fish compared with the control fish (electronic supplementary material, figure S2), suggesting that these fish showed some attraction to jellyfish but failed in most cases to successfully bond.

The mean number of attempts to associate with jellyfish was also approximately three times lower (t-test, t31 = −3.173, p = 0.003) for CO2-treated compared with control fish (figure 2b). Of all fish, only 63% of the individuals from the high-CO2 treatment associated with jellyfish (binomial test, p = 0.096), whereas in the control treatment 86% (p = 0.006) associated with jellyfish.

Yellowtail scad held in ambient seawater conditions were deterred by jellyfish olfactory cues in the flume choice test (figure 2c; p = 0.002). The same was true for high-CO2-treated larval mulloway (Argyrosomus japonicus) (p < 0.001) and for...
CO₂ through the same neurological pathway, leading to modified behavioural responses, such as altered risk perception of poisonous jellyfish tentacles or reduced recognition of jellyfish as a potential host. Alternatively, elevated CO₂ could make fishes less fearful of potential predators [36,39], venturing further away from protective shelter [23], and thereby weakening the close association with the jellyfish and its protective tentacles.

The fish–jellyfish association does not appear to be driven by olfactory cues under ambient (present-day) pCO₂ conditions. Our control flume choice experiment revealed that none of the three fish species tested were attracted towards jellyfish olfactory cues, and in most cases were deterred by the cue. This is consistent with previous observations for larval barramundi (deterrence) and for mud crab larvae and juvenile shrimp (both: no response) towards olfactory cues of the same jellyfish species [21]. Together, these results suggest that larval fish can detect jellyfish olfactory cues but are not attracted by them. By contrast, in the choice test where fish could see (and smell) the jellyfish, yellowtail scad repeatedly approached and associated with the jellyfish. This suggests that jellyfish detection or association in nature is not driven by olfaction, but rather by other sensing such as vision, thigmotaxis or negative phototropism [8].

Altered fish–jellyfish symbiosis could potentially have important consequences for the population dynamics of the respective fish species. Fish–jellyfish associations occur in temperate as well as tropical ecosystems across more than 80 species pairs and serve as a mechanism to reduce predation on associated fish [9]. We found about a third of the jellyfish in our study area to harbour one or more juvenile fishes. It is typically juveniles of pelagic species such as scads, trevallies, medusafishes, driftfishes and butterfishes that associate with jellyfish [8]. These fish species have a pelagic lifestyle and therefore do not strongly associate with benthic habitats. In an open water environment with little protection from predators, jellyfish aggregations can provide pelagic habitat that decreases mortality during the sensitive early-life stage. Weakening of this symbiosis might thus lead to increased juvenile mortality, which might be particularly detrimental for fish species or localities where this fish–jellyfish association is common. However, further insights are needed to evaluate the degree to which the relatively small decrease in time spent near jellyfish by high-CO₂-treated fish will result in increased mortality from predation compared with non-affected fish. Yellowtail scad and several other fishes (e.g. walleye pollock, Atlantic bumpers, trevallies) that commonly associate with jellies are commercially harvested, and high-CO₂ disruption of fish–jellyfish associations could therefore have flow-on effects for fisheries. Disruption of this symbiosis could even have cascading effects on higher trophic levels, as some seabird species specifically target fishes associated with jellyfish [40], with attack rates increasing as a function of fish density among jellyfish tentacles [41].

4. Discussion

Our study is the first to show that non-coral symbiotic relationships in the ocean have the potential to be altered by ocean acidification. In a choice experiment, fish that commonly associate with jellyfish in nature approached their jellyfish host less frequently and spent less time close to their host under future high-CO₂ conditions than under present-day conditions. Most fishes associating with jellyfish do not have any immunity against jellyfish toxins [8], and therefore need to continuously adjust their position relative to the pulsating jellyfish host to avoid contact with the cnidocytes on their oral arms or tentacles [15,29]. Ocean acidification can reverse or alter a wide range of animal behaviours mediated by vision, olfaction or audition in fishes as well as invertebrates [18,30] by interfering with the brain neurotransmitter function [31,32]. The potential for acclimation and adaptation in fishes towards ocean acidification effects remains elusive [33,34]. Visual acuity [35], visual risk assessment [36], visual habitat association [37] and sheltering behaviour [38] are all altered by elevated CO₂. Hence, fish–jellyfish associations may be affected by high

**Figure 2.** Response of larval/juvenile fishes from control and high-CO₂ treatments towards visual and olfactory jellyfish cues. (a) Mean (± s.e.) time juvenile scad spent close to jellyfish and (b) number of times scad approached jellyfish, tested in an aquarium test arena. (c) Time spent by three fish species in jellyfish cue water, tested in a flume choice chamber. The dashed line shows the ‘no choice’ value based on a 50% chance of presence at either side of the flume, and asterisks show a significant choice as tested with a one-sample t-test or Wilcoxon signed-rank test. Numbers between brackets show number of replicate fish tested in control and high-CO₂ treatments, respectively.

control (p = 0.003) as well as CO₂-treated (p = 0.002) larval barramundi (*Lates calcarifer*). Mulloway larvae from the control treatment did not show any preference or deterrence to the cues (figure 2c; p = 0.411).
jellyfish would be exacerbated. Much more information about the specificity of fish–jellyfish relationships is required, as well as comprehensive understanding of jellyfish population trajectories to fully assess the implications for fish populations of a potential weakening in the fish–jellyfish symbiosis.

Experimental test arenas such as aquaria are often poor representatives of natural environments and this is reflected in our results. Control fish only spent 8% of their time in the jellyfish zone and were often swimming around. At least two potential factors might explain this behaviour: (i) the absence of a natural predator, which could have resulted in lack of a trigger to seek shelter near the jellyfish; and (ii) the fact that the fish were present in an artificial, confined environment where there was likely an increased motivation to explore the novel environment and/or search for a way out. Hence, the percentage of time associated with the jellyfish is not the ecologically most relevant response variable to evaluate the effect of high CO2 on fish behaviour. By contrast, (i) number of attempts to associate with the jellyfish and (ii) the percentage of all individuals that initiated an association are ecologically more relevant because both reflect the ability of fish to show regular association behaviour. Percentages individuals were measured on a binary scale (yes/no) and are therefore less fraught to test arena biases than per cent time (continuous scale). Of our control fish tested in the aquarium (and which were all caught in the field in association with a jellyfish) 86% re-established their association with the jellyfish showing a strong response reflective of natural behaviour. Of the high-CO2-treated fish only 63% of the individuals re-associated with the jellyfish, suggesting a true effect of ocean acidification. Number of attempts to associate with jellyfish adds a magnitude to this response by showing the degree to which fishes return to their jellyfish host after the first inspection (on average 12 times in control fish). Because this behavioural response was also reduced under high CO2 (only four times), the results for these two factors suggest an ecologically relevant response to jellyfishes by control fishes, and a negative effect under high-CO2 conditions. However, how this retarded response will scale up to population level and fishes in a natural environment needs further consideration.

By serving as hosts for a diverse suite of vertebrate and invertebrate organisms, jellyfish maintain an important role in sustaining pelagic biodiversity. Our study suggests that changing ocean conditions may impair the ability of symbionts to associate with their jellyfish hosts, with potential negative effects on pelagic biodiversity in general, and for fish in particular.

Ethics. All experiments were performed under animal ethics approvals ENV/16/14/AEC (Griffith University) and S-2013-153 (University of Adelaide) and according to the universities’ animal ethics guidelines. Data accessibility. Data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.9008g.

Authors’ contributions. I.N. and K.A.P conceived and designed the study. M.D.R., R.C.G and K.A.P. collected the data. I.N., M.D.R. and R.C.G. analysed the data. I.N. wrote the main manuscript and all authors contributed to the writing of the article.

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References


3. Hacker SD, Gaines SD. 1997 Some implications of the absence of a natural predator, which could have resulted in lack of a trigger to seek shelter near the jellyfish; and (ii) the fact that the fish were present in an artificial, confined environment where there was likely an increased motivation to explore the novel environment and/or search for a way out. Hence, the percentage of time associated with the jellyfish is not the ecologically most relevant response variable to evaluate the effect of high CO2 on fish behaviour. By contrast, (i) number of attempts to associate with the jellyfish and (ii) the percentage of all individuals that initiated an association are ecologically more relevant because both reflect the ability of fish to show regular association behaviour. Percentages individuals were measured on a binary scale (yes/no) and are therefore less fraught to test arena biases than per cent time (continuous scale). Of our control fish tested in the aquarium (and which were all caught in the field in association with a jellyfish) 86% re-established their association with the jellyfish showing a strong response reflective of natural behaviour. Of the high-CO2-treated fish only 63% of the individuals re-associated with the jellyfish, suggesting a true effect of ocean acidification. Number of attempts to associate with jellyfish adds a magnitude to this response by showing the degree to which fishes return to their jellyfish host after the first inspection (on average 12 times in control fish). Because this behavioural response was also reduced under high CO2 (only four times), the results for these two factors suggest an ecologically relevant response to jellyfishes by control fishes, and a negative effect under high-CO2 conditions. However, how this retarded response will scale up to population level and fishes in a natural environment needs further consideration.

By serving as hosts for a diverse suite of vertebrate and invertebrate organisms, jellyfish maintain an important role in sustaining pelagic biodiversity. Our study suggests that changing ocean conditions may impair the ability of symbionts to associate with their jellyfish hosts, with potential negative effects on pelagic biodiversity in general, and for fish in particular.

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