The role of changing pH on olfactory success of predator–prey interactions in green shore crabs, *Carcinus maenas*

Bryce Richardson · Holly Martin · Helga Bartels-Hardege · Nichola Fletcher ·
Jörg Detlef Hardege

Abstract Arguably climate change is one of the biggest challenges faced by many organisms. One of the more significant of these is the decreasing pH level of the ocean, a consequence of the increasing amount of atmospheric CO_2 being absorbed. With the current open ocean pH level of 8.15 projected to fall to just over 7.6 in 2100, the impacts could be devastating for marine species reliant upon olfaction to survive. Here, we show that *Carcinus maenas* (shore crab) can detect and respond to the presence of odour cues from predatory species with no significant change between both current and projected pH conditions. In contrast, *C. maenas* ability to detect and respond to prey cues is altered in the projected climate change conditions, with a delayed response being observed at pH 7.6. A difference can be seen between males and females, with males detecting prey cues faster than females in reduced pH, suggesting the potential for males to be better acclimated to future climate change conditions. The change in ocean chemistry is postulated to have a fundamental impact on chemical communication systems in aquatic species. Here, we show such negative impacts of altered pH on feeding responses in *Carcinus maenas*, a typically robust keystone intertidal species and confirm that not all behaviours are affected equally with potentially significant implications for such functional traits and species interactions.

Keywords Predator–prey interactions · Ocean acidification · Olfactory disruption · Chemical ecology

B. Richardson · H. Martin · H. Bartels-Hardege ·
N. Fletcher · J. D. Hardege (✉)
Department of Biological and Marine Sciences, The University of Hull, Cottingham Road, Hull HU6 7RX, UK
e-mail: j.d.hardege@hull.ac.uk

Introduction

The increase in temperature and carbon dioxide associated with climate change have been attributed to anthropogenic activities and the combustion of fossil fuels (Gattuso et al. 2015) and is expected to represent a major challenge for marine life. Since the beginning of the industrial revolution, atmospheric CO_2 has risen from approximately 270 parts per million (ppm), to around 384 ppm in 2005 (Solomon et al. 2007), and 412 ppm in March 2020 (ESRL Global Monitoring Division—Global Greenhouse Gas Reference Network 2020). The increasing amount of CO_2 within the atmosphere is resulting in greater volumes being absorbed by natural carbon stores such as the oceans, with an estimated 30% of anthropogenic CO_2 having already been absorbed (Hoegh-Guldberg

et al. 2018; Rhein et al. 2013). These rising CO_2 levels are leading to changes to the long-standing carbon chemistry of the oceans via a process known as ocean acidification, lowering the pH of the oceans (Caldeira and Wickett 2003).

The pH of the oceans has already fallen by 0.1 compared to the pre-industrial age and is continuing to decrease further by another 0.4 to around 7.6 by 2100 (Orr et al. 2005; Bindoff et al. 2019). Changes to the pH level in marine ecosystems have been shown to impact and force marine organisms to attempt adaptation to a lower pH environment (DeWeerdt 2017). The projected pH values for the mid and end of this century have been forecast to cause an increase in the intensity of coral bleaching, and a 5% decline in calcification rates of coral by 2034, meaning corals will struggle to deposit calcium carbonate resulting in smaller, less species dense reefs (Albright and Langdon 2011; Crook et al. 2011; van Hooidonk et al. 2013). This impact on calcification rates will impact numerous other calcifying species such as crustaceans—as calcification is used in the moulting process to harden the new exoskeleton (Luquet 2012).

Multiple research papers (see Clements and Hunt 2015 for review) suggest there is also disruption to olfactory behaviours in fish and invertebrates as a result of lowered pH levels (Wyatt et al. 2014). Orange Clown Fish (*Amphiprion percula*) larvae struggled to find reef habitats and suitable settlement sites (Munday et al. 2009). Dixson et al (2010) found that in projected pH conditions, *A. percula* became strongly attracted to odour cues of natural predators, suggesting that a number of essential olfactory responses are inhibited or altered within this species as well as in predatory fish (Draper and Weissburg 2019 for review). It has been noted that the ability to detect prey was significantly inhibited in reef predators such as the Brown Dottyback, *Pseudochromis fuscus* (Cripps et al 2011). Similarly, Dixson et al (2014) investigated the impact of the expected pH conditions for 2100 on the Smooth Dogfish, *Mustelus canis*, with results showing the individuals subjected to the lower pH condition avoided odour cues associated with food.

The effects of rising oceanic CO_2 and the related reduced seawater pH on a large range of aquatic organisms' predator–prey interactions are now widely accepted (DeWeerdt 2017; Draper and Weissburg 2019). However, further work is required to investigate the effects of such conditions on keystone species on a global ecological scale, especially in variable environments such as estuaries and where multiple behaviours can be tested. Here, we have focused on one of the world's most successful invasive species, the Green Shore Crab, *Carcinus maenas* (Lowe et al. 2000) that inhabits coastal ecosystems and is known to be impacted by extreme pH conditions (Carstensen and Duarte 2019) such as experienced in tidal pools (Briffa et al. 2012). Like most marine invertebrates (Hay 2009) shore crabs rely significantly on chemical cues to gain information on their environment and to coordinate key behaviours including reproduction, foraging and detection of predators (Hayden et al. 2007; Hardege et al. 2011a). With shore crabs inhabiting environmentally variable coastal areas where temperature, salinity, pCO_2 and pH change greatly on a daily and seasonal basis (Baumann et al. 2015), *C. maenas* was chosen to examine if a degree of adaptation to low pH on olfactory sensitivity exists. In predator–prey olfaction it could also be expected that cues of high survival values, here the odour of a predator are less affected by environmental factors than feeding cues (Draper and Weissburg 2019). Here, we investigated how successfully *C. maenas* can detect its prey, the blue mussel (*Mytilus edulis*), and a predator, the common cuttlefish (*Sepia officinalis*), in present day pH of 8.2, and predicted pH condition for the year 2100 of pH 7.6.

Materials and methods

Experimental animals

During October 2018 and 2019, a mixture of male and female adult shore crabs, *Carcinus maenas*, varying similarly in size between 3 cm and 5.5 cm carapace width were collected from the intertidal zone of Esteiro Do Ramelhete (Faro, Portugal). Animals are deemed adults and sexually mature from a carapace width of at least 3.0 cm (Berril 1982) or when found in mating pairs in the initial 4 × 1 x1m holding tanks. Animals were kept in 4 large tanks (1 m x 1 m x 1 m) with a constant flow of seawater at an average temperature of 19.9 °C across all experimental days. Two tanks were at pH 8.15 and two at pH 7.6 and for each pH tanks were for either pre- or post-bioassay keeping. Those crabs in the post-bioassay tanks were not re-used for 24 h to avoid learning of odours. Each

tank had ample hiding tubes so that crabs were able to have individual shelters. A week prior to the beginning of the study, the crabs were separated into these two experimental groups in the communal tanks ($N = 150$ per tank) designed to pick crabs at random to avoid pseudo-replication.

Group one remained in a flow through tank with natural pH 8.15 seawater, and the others were placed in a tank with a flow through of carbon dioxide treated seawater at pH 7.6 seawater to acclimatize crabs for use during the study (Sordo et al. 2016). The automatically controlled system enabled to have a pH value of 7.6 achieved by having CO_2 pumped through the natural seawater, acquired from the estuary all crabs were sourced from, until the desired value was reached. Prior to the bioassays individuals were sexed, and any specific characteristics recorded, such as lack of appendages, or the presence of eggs. Only crabs with no apparent damage (e.g. missing chaelae) were included to reduce the impact of difference in physiological status of the crabs upon their behaviour. The animals were fed ragworms, *Nereis diversicolor,* the week prior to the beginning of the study and starved from this day to ensure a reaction to a prey cue would occur, as reactions to food stimuli are known to depend on appetite and shore crabs can starve for over a month (Wallace 1973).

Olfactory cues

For this study, two natural odour cues were used throughout: the odour of a Common Cuttlefish (*Sepia officinalis*), and the odour of Blue Mussels (*Mytilus edulis*). The odour cue of *S. officinalis* was sourced by sampling water from a tank containing 30 adult cuttlefish individuals, 15 males and 15 females, within 3000 L of flowing natural seawater from the culture system at the Ramalhete field station. This was taken fresh from the tank at the same time each day to ensure the odour cue was present and as much as possible at the same concentration each day. For the prey cue, *M. edulis* were purchased as fresh local catch, these were then crushed, and 1 millilitre of the tissue fluid produced was mixed with 9 millilitres of filtered natural seawater in order to create the odour of injured prey.

Behavioural assays

Randomly selected crabs were isolated individually in a tank (45 cm x 15 cm and 3 cm depth of required pH seawater, sides darkened to avoid light stimulation from surroundings), using a plastic ring (approximately 6 cm diameter, 5 cm height) covered by a tile. This was used to avoid any impact from the introduction of the visual stimuli at either side of the container. Furthermore, the ring was used to ensure any visually induced movements involved with adding the odour cue were avoided. Using an Eppendorf M4 multipette, 0.5 ml of the required cue solution was added to a sponge (previously washed with alcohol and rinsed with seawater), an object usually not attractive to crabs (Hardege et al. 2011a) and placed inside a metal nut, approximately 1 cm wide. The side of the tank with the cue was chosen at random and a control was added to the opposite side in form of a sponge filled nut without a cue (see Fig. 1).

Once the cue was injected into the randomly chosen sponge and allowed to disperse within the water for 10 s, the ring was removed enabling the animals to move freely in the tank. Behaviour was observed for a further two minutes for the predator cue, and for 5 min for the prey cue. Response to the prey cue was determined as an attempt to feed on the sponge with the feeding stimuli. A positive reaction to the predator cue was determined by two behaviours; a freeze response, meaning the individual stopped moving for more than 2 s, and a retreat response, which occurred when the individual's carapace touched the opposing side of the container to the location of the predator cue. Once the individual had been observed, the sponges were removed and thoroughly rinsed using natural sea water from the same source as that within the tanks to
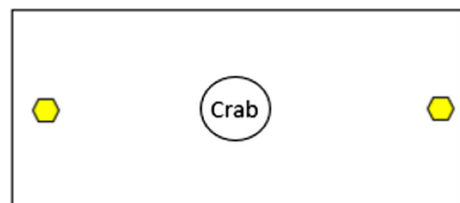

Fig. 1 The experimental set up used during the study, showing the crab (*C. maenas*) isolated in the centre of the container (45 cm × 15 cm × 15 cm) by a plastic ring (6 cm diameter), and the two visual stimuli either side; one of which was chosen at random to contain 0.5 ml of the required odour cue

ensure none of the odour cue was present prior to the next individual being tested.

The figures show the time required for a crab to respond to the cues presented. It does not show the duration of the reaction as for the purposes of the study this was not relevant. We only measured the time taken to detect the presence to determine if pH was impacting the olfactory ability of the species. Fathala et al. (2009) showed that crustaceans have the ability to form short term memory if subjected to the same conditions repeatedly for a short period of time (under 30 min). To ensure this would not impact the study, individuals were placed in a separate 1 m × 1 m × 1 m tank containing the designated pH water after observation and not tested again until the next day.

Statistical analysis

Statistical analysis was conducted using the IBM SPSS statistical analysis software (version 25). The data sets were initially tested for normality using a Shapiro–Wilk test. All data sets had a p-value below 0.05, meaning nonparametric tests were needed as the null hypothesis of the data being normally distributed is rejected. A comparison of the mean values was then conducted using a Mann–Whitney U test, to determine if there is a significant difference between the mean values, and from this, whether the null hypothesis can be rejected or not.

Results

During the control bioassays without addition of olfactory cues, *C. maenas* acclimated to both present day and future pH conditions, moved around the bioassay container frequently, with limited time remaining still. Few individuals attempted to feed on the visual stimuli (15%, $n = 20$, 10 per pH condition). Escape and freeze behaviour associated with the presence of a predator occurred, albeit after an initial period of movement around the container in 16 of the 20 control tests.

When testing with the presence of a prey cue (*Mytilus edulis*), the crabs acclimated at pH 8.2 found the presence of the prey cue significantly quicker than those acclimated at pH 7.6 (Fig. 2, $p = 0.002$, $n = 45$ and 38 in pH 8.2 and 7.6 respectively). In present day conditions, males found the presence of the prey cue

significantly quicker than females, however in projected pH conditions for the year 2100, there was no significant difference in the time taken to find the presence of the prey cue between males and females (Fig. 3, $p = 0.043$, $n = 45$, and $p = 0.342$, $n = 38$ respectively).

When subjected to the odour cue of a predator (*Sepia officinalis*), the different pH conditions had no significant impact upon the ability to detect and respond to the presence of predator odour (Fig. 4, $p = 0.85$, $n = 116$). Differences between sexes were also compared for the presence of the predator cue, showing no difference between males and females, in either the present-day condition (pH 8.2), or projected conditions for 2100 (pH 7.6) (Fig. 5a/b) $p = 0.806$, $n = 60$ and B) $p = 0.576$, $n = 55$ respectively).

Discussion

As *Carcinus maenas* naturally encounter fluctuating pH and temperature conditions in the intertidal zone, and are known to be only affected significantly in very low pH conditions (Briffa et al. 2012), we expected that the instinctive detection of especially a predator and to a certain extent also of prey presence would be largely uninhibited by the year 2100 pH conditions (pH 7.6). However, as shown above, the results of this study suggest otherwise, with individuals subjected to projected pH conditions of 7.6 taking significantly longer to detect the presence of a prey odour cue than those acclimated to present day pH conditions of 8.2 (Fig. 2). Males were also shown to be able to detect the presence of a prey cue significantly quicker than females in present day conditions, but no difference was shown in projected conditions (Fig. 3). Results also suggest decreasing pH levels associated with climate change have no impact upon *C. maenas*' ability to detect and respond to the presence of predator odour (Fig. 4). Respiration data also support this, showing that oxygen consumption in crabs increase significantly upon predator odour exposure independent of seawater pH (see supplementary material).

Previous studies into predator–prey interactions have found similar results in other species, such as Blue Crabs, *Callinectes sapidus* (Glaspie et al. 2017), Korean Common Dogwhelks, *Thais clavigera* (Xu et al. 2017), European Seabass, *Dicentrarchus labrax*
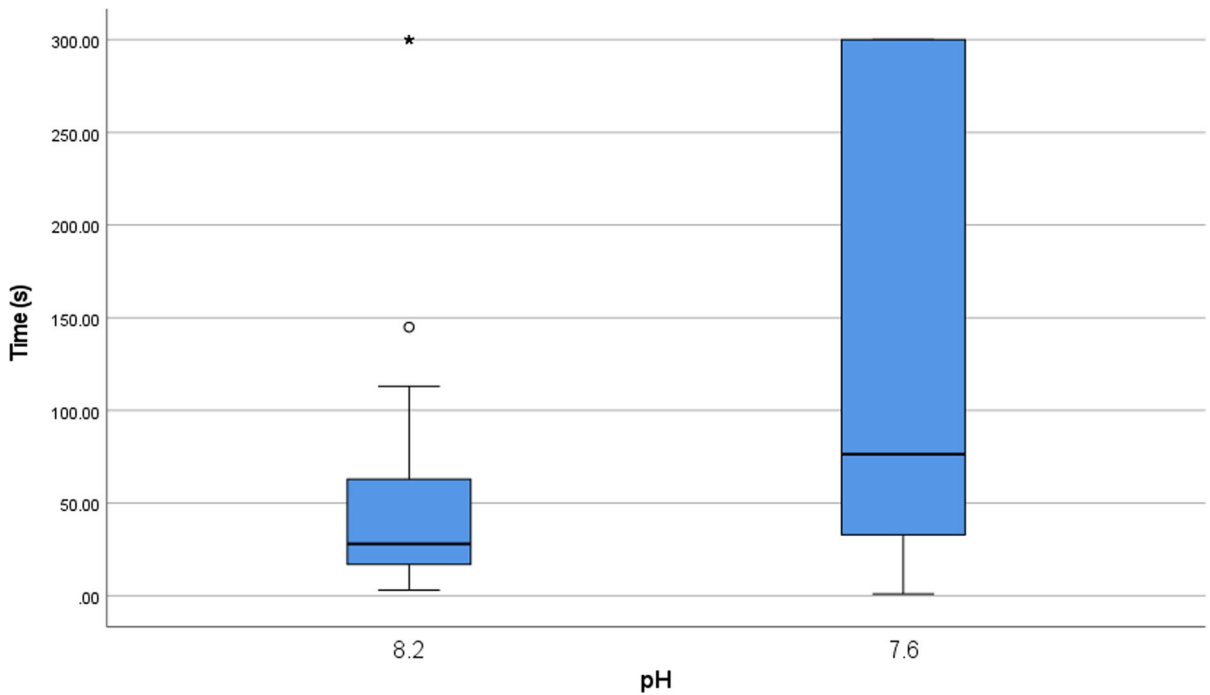
Fig. 2 Distribution of results in time taken (s) for *Carcinus maenas* to find a prey cue (*Mytilus edulis*) in both current pH conditions, (8.2), and those projected for 2100 (7.6). pH 8.2: $n = 45$, mean = 67 s $\pm$ 13 s; pH 7.7: $n = 38$, mean = 46 s $\pm$ 21 s; $p = 0.002$
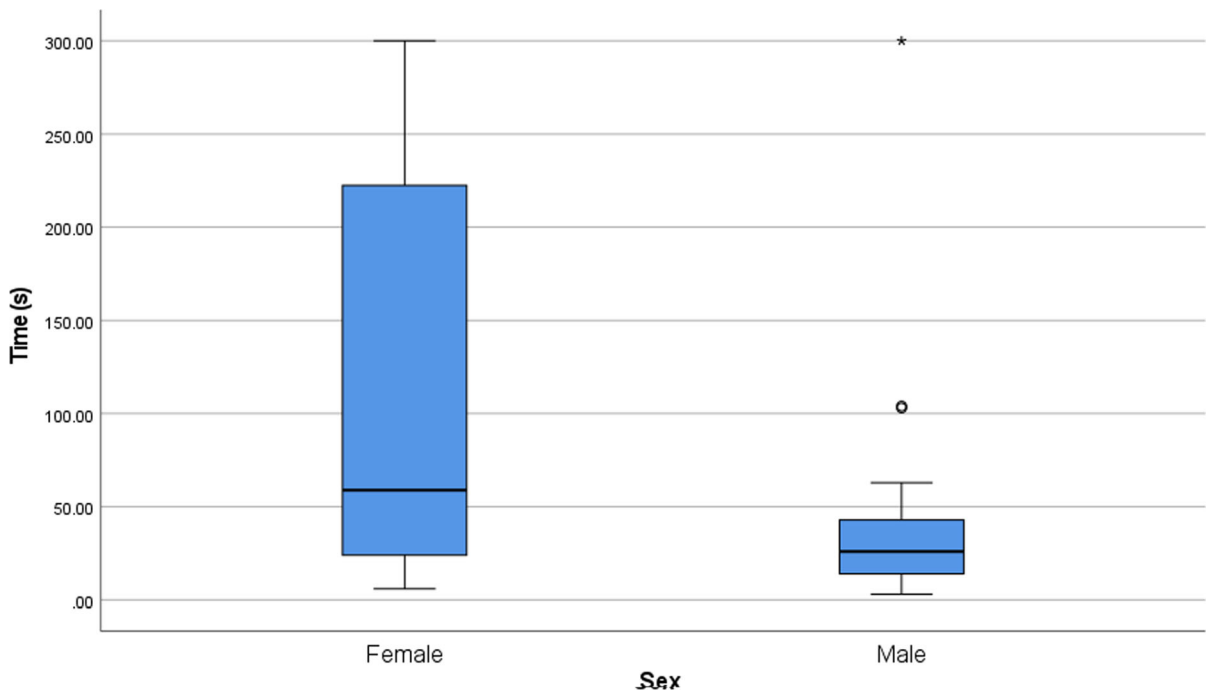

Fig. 3 Distribution of results for males and females in time taken (s) for *Carcinus maenas* to find the presence of a prey cue (*Mytilus edulis*) in current pH conditions (8.2). Female: $n = 15$, mean = 118 s $\pm$ 31 s; Male: $n = 30$, mean = 41 s $\pm$ 10 s. $p = 0.043$
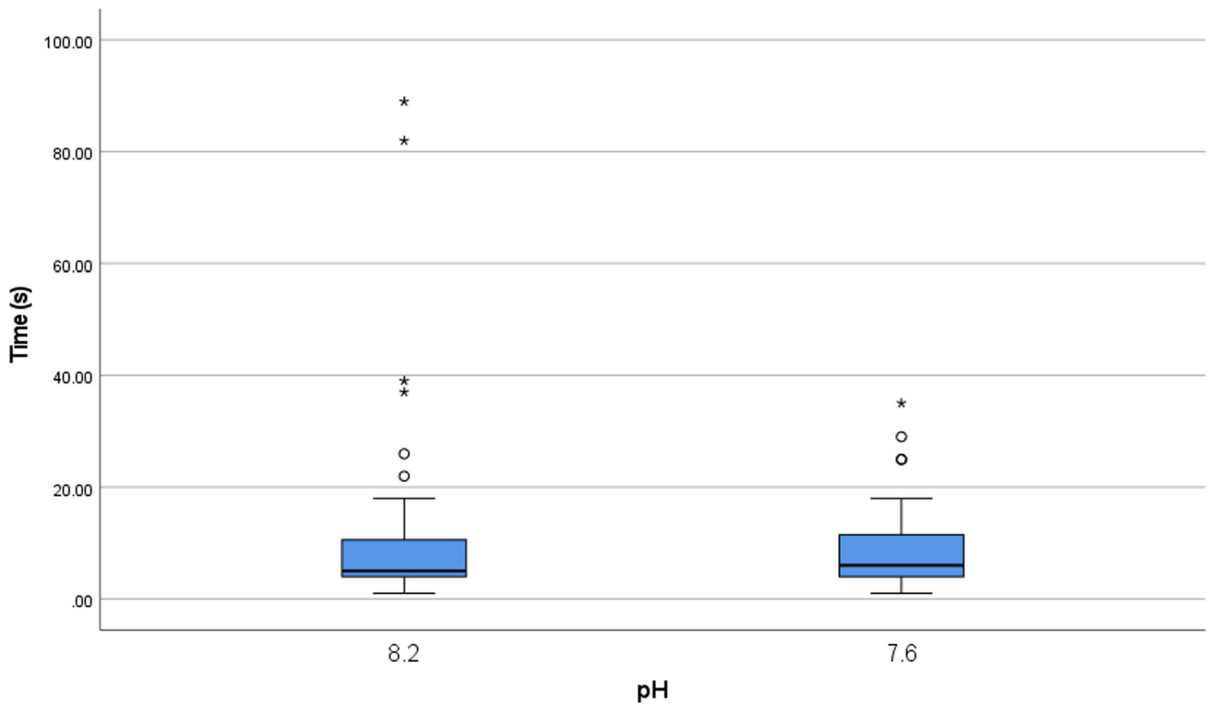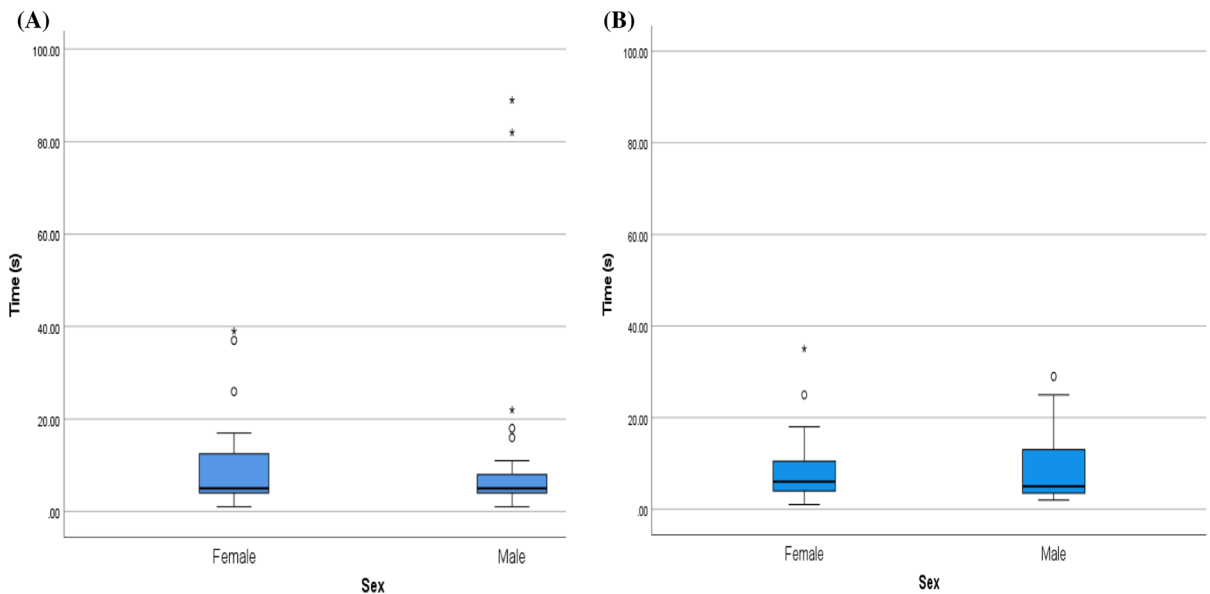
Fig. 4 Distribution of results in time taken (s) for *Carcinus maenas* to react to the presence of a predator odour (*Sepia officinalis*) in both current pH conditions (8.2), and those projected for 2100 (7.6). pH 8.2: $n = 61$, mean = 11 s $\pm$ 2 s; pH 7.6: $n = 55$, mean = 8 s $\pm$ 1 s. $p = 0.85$

(A)

(B)

Fig. 5 Distribution of results in time taken (s) for male and female *Carcinus maenas* to react to the presence of a predator odour (*Sepia officinalis*) in A) current pH conditions (8.2), and B) in projected pH conditions for the year 2100 (7.6). **a** Female: $n = 32$, mean = 9 s $\pm$ 2 s; Male: $n = 28$, mean = 12 s $\pm$ 4 s. $p = 0.806$. **b** Female: $n = 28$, mean = 9 s $\pm$ 1 s; Male: $n = 27$, mean = 8 s $\pm$ 1 s. $p = 0.576$

(Porteus et al. 2018) and Mud Crabs, *Panopeus herbstii* (Dodd et al. 2015) all showing reduced olfactory range of up to 40%, reduced olfactory success and reduced foraging behaviours in conditions synonymous with the end of the century (Wang et al. 2018). Some authors suggested that alterations of behaviours under increased CO_2 and decreased pH levels have been attributed to olfactory disruption through the alteration of neurotransmitters such as gamma aminobutyric acid (GABA) (Nilsson et al. 2012), which is crucial also to the function of invertebrate central and peripheral nervous systems (Briffa et al. 2012; Lunt 1991). Briffa et al (2012) highlighted that in the shore crabs haemolymph ionic concentrations are not changing when crabs are exposed to low pH conditions. This makes it unlikely that changes to neurotransmission of cues is the key factor in the observed alterations to prey odour, especially since the predator odour responses in the crabs were unchanged.

As well as the changes to neurotransmitters, ocean acidification has also been shown to have the potential to cause changes to the structure of signalling cues such as peptides through altered protonation (Hardege et al. 2011b; Roggatz et al. 2016, 2019). These changes to the receptor-ligand interactions could cause an organism to take longer to detect an odour or become completely unable to sense the presence of an odour as the bioavailability of the correct form of the olfactory cue is reduced (Velez et al. 2019; Roggatz et al. 2019).

The slower reaction to prey odour cues could also be attributed to the physiological impact of climate change conditions, for example upon respiration, and the resulting reduced activity rates. Paganini et al (2014) found that extreme pH and temperature conditions projected by the Intergovernmental Panel on Climate Change (IPCC) negatively impact the respiration rates of crustaceans, in this case the porcelain crab (*Petrolisthes cinctipes*). This reduction in respiration caused reduced activity states, which has been linked to reduced sensitivity to the presence of food cues (Zimmer-Faust et al. 1996) albeit this would not fully explain why the shore crab's perception and response to predator odour is unchanged (Fig. 4). There are clearly several ways in which ocean acidification has been shown to have negative impacts on marine organisms' abilities to detect the presence

and location of food, which are supported further by the results of this study.

Despite the difference shown in behaviour in the presence of the odour of prey, the results suggest that the impact of low pH conditions has no significant impact on *Carcinus maenas'* ability to detect the presence of a predator (Fig. 4). Weissburg and Zimmer-Faust (1994) found that *Callinectes sapidus* rely heavily on spatial and temporal aspects of an odour cue. As the odour cue of the predator, *Sepia officinalis*, was taken each morning, the temporal aspect of the odour cue could have led to a reduction in the defensive response from *C. maenas* as shown by the results in this study. Results from previous studies have shown that odour cues which are not sourced within a maximum of 30 min decay, leading to a reduction in the defensive response elicited to the odour cue later in the day, as the predator odour was sourced in the morning (Ferrari et al. 2007; Bytheway et al. 2013; Chivers et al. 2013). Variability in the quality of an odour cue obtained through conditioning water, in this case predators, is a major contributor to experimental variance in the behavioural responses of the cue receiver in any biological assay. This is especially important when the signal is a bouquet of multiple chemicals where some may be more affected by reduced pH than others (Roggatz et al. 2016; Hardege et al. 2011b). Feeding stimulants are often a complex array of diverse molecules including amino acids, nucleosides, fatty acids and other lipophilic compounds and their ratios may also vary (Velez et al. 2019). The use of synthetic chemical signals allows for controlled, precise dosing of cues in biological assays enabling dose–response curves and the determination of response thresholds that then allow to examine small changes in signal detection and animal responses over pH (Hardege et al. 2011b; Roggatz et al. 2016, 2019).

Other factors have also been shown to impact how an odour cue is interpreted and what response is caused. Weissburg and Beauvais (2015), and Poulin et al (2018) found that the diet of a predator has an impact upon how prey species respond to the presence of its odour cue. The predator odour cue used in this study was sourced from *S. officinalis,* which had been fed with shrimp. This absence of *C. maenas* within the diet of the cuttlefish used could explain a lack of, or greater time taken to display a defensive response, but from Fig. 5 it is evident that the crabs did detect and

respond to the cuttlefish odour. Cattano et al (2017) found that in the family of fish known as wrasse, temperate alterations did not change the ability to detect the presence of predators; which alongside the results of Andrade et al (2018) that showed no change to the behaviour of speckled sanddab (*Citharichthys stigmaeus*) in elevated CO_2 conditions suggest there is also the potential for climate change conditions to affect olfaction more substantially in different species.

The differences shown between the time taken for males and females to detect the presence of a prey cue suggest there could be physiological or morphological differences between sexes. As shown by Hayden et al (2007) shore crabs' responses to feeding stimulants vary between the sexes specifically throughout the seasons with males requiring higher doses of feeding stimulants during the summer reproductive season whilst in autumn/winter both sexes responded equally. With the data in the present study collected in late October, at the end of the reproductive season it is feasible to assume male responses were heightened after a summer period of reduced intake of prey. Spooner et al (2007) found preferences for food between sexes in *C. maenas*, which could explain why males were more reactive to the presence of *M. edulis*, as physiological differences in chelae size would result in less energy being used by a male in order to crack the shell of *M. edulis*. However, no significant difference was shown between sexes in the ability to detect the presence of a predator. As both sexes are equally at risk of predation, it is unlikely that there would be any difference in the ability to detect the presence of a predator (Fig. 5a and b).

In conclusion, results from this study into the impacts of ocean acidification upon the olfactory abilities of marine organisms show the potential for serious implications altering predator–prey interactions. However, it is still unclear exactly how accurately these results can be compared to naturally occurring behaviours and conditions. Naturally occurring diel CO_2 conditions show the impacts of climate change conditions are less substantial than those of stable reduced pH and elevated CO_2 conditions used in many studies (Jarrold et al. 2017), presumably because the higher pH during the daytime enabled animals to detect and respond to odour cues. Goldenberg et al (2018); who found that in more complex natural environments, compared to laboratory test settings, behaviours showed fewer changes to elevated CO_2

levels. Despite these studies and the results shown by *C. maenas* here, our understanding how ocean acidification will impact complex linked functional traits, is still nowhere near sufficient to predict ecosystem responses. Further research is required to determine how climate change will impact ecosystem services on a larger, multi-generational scale, as well as in field studies. Our data suggest *C. maenas'* olfactory cue-based predator–prey interactions are altered in the pH conditions projected by the end of the century, impacting the complex species interactions governed by olfactory cues.

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