ICES Journal of Marine Science

ICES Journal of Marine Science (2016), 73(3), 613–619. doi:10.1093/icesjms/fsv019

Contribution to Special Issue: 'Towards a Broader Perspective on Ocean Acidification Research'

Original Article

CO_2-driven decrease in pH disrupts olfactory behaviour and increases individual variation in deep-sea hermit crabs

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Kim, T. W., Taylor, J., Lovera, C., and Barry, J. P. CO_2-driven decrease in pH disrupts olfactory behaviour and increases individual variation in deep-sea hermit crabs. – ICES Journal of Marine Science, 73: 613–619.

Received 18 September 2014; revised 18 January 2015; accepted 20 January 2015; advance access publication 16 February 2015.

Deep-sea species are generally thought to be less tolerant of environmental variation than shallow-living species due to the relatively stable conditions in deep waters for most parameters (e.g. temperature, salinity, oxygen, and pH). To explore the potential for deep-sea hermit crabs (*Pagurus tanneri*) to acclimate to future ocean acidification, we compared their olfactory and metabolic performance under ambient (pH ~7.6) and expected future (pH ~7.1) conditions. After exposure to reduced pH waters, metabolic rates of hermit crabs increased transiently and olfactory behaviour was impaired, including antennular flicking and prey detection. Crabs exposed to low pH treatments exhibited higher individual variation for both the speed of antennular flicking and speed of prey detection, than observed in the control pH treatment, suggesting that phenotypic diversity could promote adaptation to future ocean acidification.

Keywords: hermit crabs, individual variation, ocean acidification, olfactory function, prey detection.

Introduction

Future ocean pH is projected to drop considerably at all depths as the rising inventory of atmospheric CO_2 is absorbed by surface waters and mixed to depth. This phenomenon of ocean acidification is a growing concern for the health of marine ecosystems (Orr *et al.*, 2005; Doney *et al.*, 2009). Owing to the accumulation of respiratory CO_2, the pH of deep ocean waters is generally lower than in surface waters (Feely *et al.*, 2008; Brewer and Hester, 2009). Under the SRES A1B scenario, the pH of deep-sea waters (ca. 1000 m) is expected to decrease by 0.2–0.4 units by the end of the 21st century (Ilyina *et al.*, 2010), and under the RCP 8.5 scenario, with larger CO_2 emissions, bathyal pH could decrease even more. Environmental hypercapnia and associated changes in deep-sea carbonate chemistry could affect physiological processes that contribute to the individual performance of deep-sea animals and ultimately to population survival. Though deep-sea animals are assumed to be physiologically adapted to the pH of their habitat depth (typically lower than surface waters), several studies indicate that further reduction in pH can be more stressful for deep-sea taxa than related upper ocean species (Seibel and Walsh, 2003; Pane and Barry, 2007; Pane *et al.*, 2008). Deep-sea animals are generally thought to be less tolerant of environmental changes (such as future ocean acidification) than shallow-living taxa because of the environmental stability (oxygen, temperature, pH, etc.) of deep-sea waters (Pane and Barry, 2007; Smith *et al.*, 2009).

Although some taxa may acclimatize to high environmental CO_2 levels (Ries *et al.*, 2009; Kroeker *et al.*, 2010), their physiology and behaviour may be affected, leading to potentially adverse impacts on their individual performance (Portner, 2008; Munday *et al.*, 2010; Briffa *et al.*, 2012; Sung *et al.*, 2014). Environmental hypercapnia can alter the metabolic rates of organisms (Bibby *et al.*, 2007; Wood *et al.*, 2008). It can also weaken olfactory functions of animals (de la Haye *et al.*, 2012; Nilsson *et al.*, 2012) and thus deter homing ability (Munday *et al.*, 2009), predator/prey detection (Munday *et al.*, 2009; Dixson *et al.*, 2010; Cripps *et al.*, 2011), resource assessment, and decision-making (de la Haye *et al.*, 2011). Exposure to low seawater pH can also affect the defensive abilities of prey species, perhaps rendering them more vulnerable

to potential predators (Bibby *et al.*, 2007). Such sensory and behavioural changes due to ocean acidification can alter the ecological function or role of some marine organisms and potentially affect the structure and function of marine communities (Briffa *et al.*, 2012).

Variation in responses to elevated environmental CO_2 within populations is another key factor concerning the response of marine species to ocean acidification. Although environmental change may cause significant negative impacts on most individuals' performance, tolerance by a subset of the population may promote adaptation for population persistence (Charmantier *et al.*, 2008; Sih *et al.*, 2012). Furthermore, behavioural differences among individuals (i.e. "personality") within populations (Sih *et al.*, 2004) can play an import role in determining the evolutionary and ecological consequences of human-induced rapid environmental changes (Sih *et al.*, 2011, 2012). High variation among individuals in response to elevated CO_2 has been shown to represent genetic diversity in some marine populations (Langer *et al.*, 2006; Pistevos *et al.*, 2011; Sunday *et al.*, 2011; Schlegel *et al.*, 2012; Kim *et al.*, 2013), but there was no evidence for individual variation in behavioural responses to high CO_2 (e.g. Munday *et al.*, 2009; Dixson *et al.*, 2010; Cripps *et al.*, 2011; de la Haye *et al.*, 2011).

The capacity for deep-sea organisms to adapt to lower pH conditions is largely unknown. Here, we investigate the influence of exposure to reduced pH waters on the behavioural and physiological function of the deep-sea hermit crab *Pagurus tanneri* (Benedict, 1892). *Pagurus tanneri* inhabits shells of *Neptunea* sp. or *Bathybembix bairdi*, and as benthic scavengers are a major consumer of organic debris on the continental slope (Ramsay *et al.*, 1997). In the dark, deep-sea environment, olfaction is likely their principal mode of food detection.

To determine if olfactory behaviour in *P. tanneri* is affected by ocean acidification, and to measure the range of variability in responses among individuals, experiments were conducted to evaluate several hypotheses. First, we tested whether the antennular flicking behaviour of *P. tanneri* is influenced by low pH. Antennular flicking is the equivalent of "sniffing" to detect chemical cues in a wide variety of decapod crustaceans including hermit crabs (de la Haye *et al.*, 2011). Therefore, this sensory behaviour was used as an indicator of olfactory ability. Second, we evaluated the hypothesis that exposure to low pH waters impairs the speed of prey detection by *P. tanneri*. We expect that the rate of antennular flicking is coupled to olfaction ability, such that a reduction in flicking rate will reduce or slow olfaction, consequently increasing the time required to detect and find prey. Finally, we measured rates of oxygen consumption to test the hypothesis that any behavioural changes in *P. tanneri* that are affected by pH are coupled to metabolic rate.

Methods

Collection and maintenance of *P. tanneri*

Hermit crabs were collected in October 2011 at 884 m depth in Monterey Bay (36.71°N 122.28°W) using a suction sampler on the Remotely Operated Vehicle (ROV) *Doc Ricketts* (Dive DR306), operated from the RV *Western Flyer* by the Monterey Bay Aquarium Research Institute (MBARI). A total of 32 individuals were collected and stored in a closed box on the ROV. Upon recovery of the ROV to the surface, specimens were transferred carefully to an ice cooler (57 l) with seawater at *in situ* temperature (5°C), pH 8.0, and 100% oxygen saturation in a thermally controlled (5°C) environmental chamber on the *Western Flyer* (5°C, pH 7.6, and DO 30 μM, were *in situ* seawater values at their depth of collection). Upon arrival at Moss Landing on the same day, the crabs were moved to an aquarium (60 × 30 × 35 cm) with replenishing seawater (5°C, 100% saturated with normal oxygen levels, and pH 8.0) flow in the dark wet seawater lab at MBARI.

Pagurus tanneri tolerated the holding conditions without any outward indication of stress. On 30 November, all crabs were fed to satiation with chopped frozen squid acquired from local fish market. Each crab was assigned to a 1 l transparent glass jar, coded, and assigned randomly to one of two pH treatment groups ("Control" or "Low-pH"). Chilled (5°C) ambient (100% saturated with normal oxygen levels, pH 8.0) seawater from a gas-controlled, flow-through aquarium system (see below) was delivered to each jar at 60 ml min^{-1}. Thirty-two jars (each housing 1 crab) were divided among 6 small (10 l) aquaria overflowing with treatment water. On the following day, claw size and shell length of each crab were measured using digital callipers. No differences were detected between pH treatment groups in either the larger claw length (Mann–Whitney *U*-test, $U = 111$, $p = 0.9504$) or shell length ($U = 108$, $p = 0.8519$). Crabs were maintained in a darkened room with only dim red light, from the time of crab placement in jars until the end of the experiment.

Seawater chemistry

Experimental conditions for seawater pH, dissolved oxygen, and temperature were maintained using a gas-controlled aquarium system, (Barry *et al.*, 2008). Oxygen (Aanderaa Inc., model 3835, www.aadi.no), pH (Honeywell DuraFET III), and temperature were logged continuously (1 Hz) using a LabVIEW (National Instruments Corp.) application. A PID-based feedback algorithm integrated with mass flow controllers (Sierra Instruments, Inc.) was used to regulate oxygen and pH in seawater reservoirs that supply experimental treatment waters.

From 1 to 5 December 2011, seawater pH delivered to both treatment groups was gradually adjusted from pH 8.0 to pH 7.6, and dissolved oxygen (DO) level was simultaneously changed from 300 to 30 μM. The pH of the Low-pH treatment group (16 jars) was then gradually adjusted from pH 7.6 to pH 7.1 between 19 and 21 December 2011. The pH of bathyal waters is expected to decrease by as much as 0.4 units by the end of the century. Therefore, pH 7.1 was regarded as a reasonable pH perturbation that the deep-sea hermit crab population may experience soon. A difference of 0.5 pH units was maintained between the Low-pH (pH 7.1) and Control (pH 7.6) treatments throughout the experiment (Table 1). Temperature and DO did not differ between treatments. Periodic measurements of pH using a spectrophotometric pH method (Byrne *et al.*, 1999; Low pH: 7.11 ± 0.01, Control pH: 7.58 ± 0.04) showed only negligible difference from measurements performed using the HoneyWell DuraFET pH sensors (Table 1). Seawater DO in each jar was also measured periodically during the experiment using Aanderraa® oxygen optodes (model 3835) to ensure the expected DO was maintained. To determine the calcite and aragonite saturation states of treatment waters, samples were collected from all treatments five times during the experiment, and dissolved inorganic carbon was measured by non-dispersive infrared analysis (LI-COR model 6262), as detailed by Friederich *et al.* (2002).

Olfaction behaviour (rate of antennular flicking)

Crabs naturally flick antennules to detect dissolved odours in seawater, and for this experiment, the rate of antennular flicking was

Table 1. Carbonate system and other physical parameters for experimental treatments measuring the response of hermit crabs (mean ± s.d.).

	Low pH	Control
pH	7.12 (± 0.02)	7.6 (± 0.01)
TCO_2	2365.57 ± 36.68	2677.67 ± 270.78
Salinity (ppt)	33.0 ± 0.1	33.0 ± 0.1
Temperature (°C)	6.0 ± 0.1	6.0 ± 0.1
PCO_2 (μatm)	3596.47 ± 159.18	1378.82 ± 111.55
Alkalinity (μEq kg^{-1})	2207.86 ± 36.19	2687.47 ± 274.02
Calcite saturation	0.36 ± 0.02	1.31 ± 0.18
Aragonite saturation	0.23 ± 0.01	0.83 ± 0.12
HCO_3^- (μmol· kg^{-1})	21 167.51 ± 35.09	2553.16 ± 258.80
CO_3^{2-} (μmol· kg^{-1})	15.00 ± 0.81	54.32 ± 7.60

The parameters were calculated with CO_2sys (Pierrot *et al.*, 2006) using the pH and TCO_2 values with dissociation constants from Dickson and Millero (1987) and KSO_4 using Dickson (1990).

recorded for each individual as the time taken for 10 flicks. No stimulus to elicit a flicking response was provided. To observe flicks clearly, a flashlight was used to illuminate the antennules. Crabs exhibited no apparent shrinking or withdrawal in response to the light, suggesting that it did not influence flicking rate. Flicking rates of each individual were measured using three separate trials from 7 to 8 December 2011, before adjusting the aquarium system to the respective treatment conditions. Once the Control and Low-pH treatment conditions were established, the rate of antennular flicking by each animal was measured once for each of 30 haphazardly selected days from 22 December 2011 to 9 May 2012 (see Figure 1 for dates of antennular flicking measurements).

Prey detection

The time required for crabs to detect and move to a food item nearby was measured under Control and Low-pH conditions during two periods: (i) 2 weeks into exposure, 5–9 January, and (ii) 4 weeks into exposure, 18–23 January 2012. Each crab from each treatment group was transferred from its jar to a 10 l test aquarium containing seawater of the appropriate treatment. The crab was then positioned in the centre of an acrylic tube (inner diameter 113 mm, outer diameter 126 mm, height 72.5 mm) standing vertically at one end of the aquarium. Using 30-cm long forceps, a portion of squid (0.2 g) was placed 3 cm from the opposite end of the aquarium, ~22 cm from the crab isolated in the acrylic tube. After 5 min, the tube was lifted from the aquarium using forceps. Each trial was then observed and recorded from outside the room using two wireless surveillance IR cameras (Foscam® model no. FI8904W). For each experimental trial, we measured the time required for the crab to locate and begin consuming the prey. If the crab failed to locate the prey within 30 min, the trial was terminated. After each trial, seawater in the test aquarium was replenished using the appropriate low- or high pH waters.

Respirometry

Oxygen consumption rates were measured for a subset (ca. 1/3) of the crabs in each group during three periods: (i) at *in situ* conditions immediately before exposure to the Control or Low-pH experimental treatments, 14–18 December; (ii) ~3 weeks into exposure, 11–15 January; and (iii) ~9 weeks into exposure, 13–16 February. For each respirometry period, five crabs were selected randomly from each treatment group. Before measurement, the shell surface of each individual was cleaned using a toothbrush. We also determined that the respiration rate of a single cleaned shell (i.e. no enclosed crab) was undetectable.

Crabs were held unfed for at least 72 h before being placed, in their shells, into one of five individual RC400 respiration chambers, each with a volume of ca. 730 ml. Each chamber was then submerged in an aquarium with seawater of the appropriate treatment chemistry, and water was allowed to circulate through the open ports of each chamber for 12–20 h before starting respiration measurements. Following this acclimation period, any small air bubbles were purged from each chamber, open ports were sealed with low surface area rubber bungs, and each was fitted with an oxygen electrode. The gas-tight chambers were then submerged inside an insulated, 5°C water bath (fresh). An oscillator (Thermolyne Bigger Bill Orbital Shaker) holding the water bath was then activated at a speed of ~25 rpm to ensure that chamber water was well mixed for accurate oxygen measurement. Oxygen was measured using microcathode oxygen electrodes and was recorded with a Strathkelvin 928 6-Channel Oxygen System (version 2.2).

Using this protocol, initial chamber O_2 levels were 60 (± 20) μM l^{-1}, and decreased due to crab respiration until O_2 in the static chamber reached 10 μM l^{-1} (3–12 h). As crabs individually reached this threshold or after 12 h (i.e. ~10% of trials), they were removed from the respirometer system and chamber, and returned to their treatment jar. Because these crabs inhabit an environment with ~30 μM O_2, we decided that respiration rates should be determined under conditions close to their environment. Therefore, the rate of oxygen consumption was calculated as a linear slope for the period when chamber O_2 levels ranged from 15 to 35 μM.

Respiration rates were scaled by the wet body mass of each crab at the end of the exposure period (determined to 0.01 g) so that O_2 consumption rates were comparable among individual as μmol O_2 g^{-1} h^{-1}. Body mass did not differ significantly between treatments (Mann–Whitney *U*-test, $U = 87.5$, $p = 0.6295$).

Ethical note

Collection of hermit crabs was approved by California Natural Resources Agency, Department of Fish and Game (Scientific Collecting Permit ID: SC-10696). There were no apparent adverse effects of bringing these crabs from the deep ocean to surface pressures—no mortality or loss of limbs during collection and transport were observed. During the experiment, a portion (~0.2 g) of chopped squid acquired at a local fishery market was given to each crab as food every 2 weeks. Some of the crabs released their larvae on February and March 2011. Therefore, we assumed the laboratory conditions were tolerable to these crabs. Six crabs (three in each treatment) died during the experiment, presumably due to asphyxiation related to failure of the water (oxygen) deliver system to their jars. At the end of the 6-month experiment, all remaining crabs were sacrificed for morphometric and body weight measurements.

Statistical analysis

The effect of pH on the rate of antennular flicking and time taken for prey detection was determined using repeated-measures analysis of variance (ANOVA). For antennular flicking rates (the number of antennular flicks min^{-1}), repeated-measures ANOVA was applied for three periods (7, 14, and 20 weeks) to determine if there was a cumulative effect of pH depending over the length of the experiment. If the assumption of equal between-group correlation and

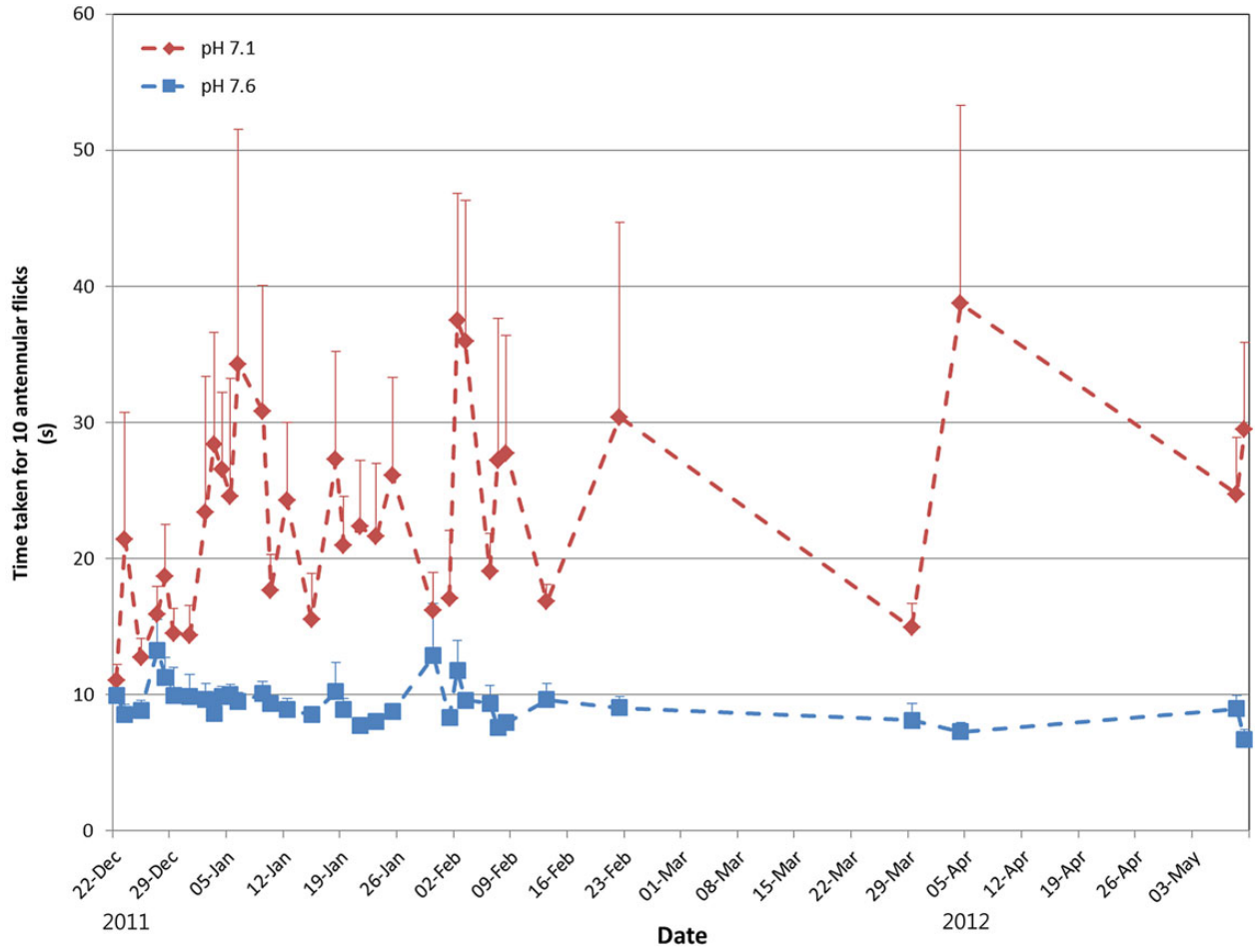

Figure 1. Time (mean ± s.e.) taken for ten antennular flicks of hermit crabs (*P. tanneri*) under Low-pH (red diamond) and Control (blue square) conditions. Crabs under Low-pH conditions required more time to flick antennules and exhibited much higher individual variation in time taken for antennular flicks than observed for crabs under Control conditions.

Table 2. Repeated-measures ANOVA results for the effect of low pH exposure on antennular flicking rates.

	7 weeks			15 weeks			20 weeks		
Source	***F***	**d.f.**	***p*-value**	***F***	**d.f.**	***p*-value**	***F***	**d.f.**	***p*-value**
Within-subject effect									
Day	1.488	25.6	0.06	1.485	29.1	0.057	1.436	33	0.058
Day × pH treatment	1.046	25.6	0.403	1.297	29.1	0.139	1.821	33	0.004
Error		487.2			552.9			495	
Between-subject effect									
pH treatment	19.323	1	<0.0001	21.137	1	<0.0001	30.219	1	<0.0001
Error		19			19			15	

variance ("sphericity") was violated (Mauchly's test, $p < 0.05$), a Huynh–Feldt correction was applied. To test for heteroscedasticity between treatments, we performed Levene's test on the average time taken for 10 antennular flicks per individual, on the time taken for prey detection 4 weeks after treatment exposure, and on respiration rates. Differences in respiration rates between treatment groups and exposure times were tested using a Mann–Whitney test because a subset (1/3) of the crabs in each groups were selected for respiration at three times and crabs were selected randomly for each treatment.

Results

Antennular flicks

The rate of antennular flicking for crabs in the Low-pH (7.1) treatment decreased through the experiment, and was significantly lower than for crabs under Control pH (7.6) after 7 days exposure to the low pH treatment (Table 2). There was a significant effect of pH treatment until the end of the experiment, whereas the effect of day or interaction between day and pH treatment was not significant until 15 weeks after exposure (Table 2).

Variation among individuals for the time required to complete ten antennular flicks was significantly higher for crabs in Low-pH seawater (pH 7.1) compared with those held in control conditions (Levine's test, $W_{1,28} = 46.028$, $p < 0.0001$, Figure 1). When we selected only one-third of all individuals from the Low-pH treatment with the shortest time for ten flicks, there was no significant difference in antennular flicking rates between treatments ($F_{1,13} = 4.468$, $p = 0.054$).

Prey detection

The time required for *P. tanneri* to detect prey did not differ between the two groups before treatment conditions (Control, Low-pH) were established (one-way ANOVA, $F_{1,18} = 0.058$, $p = 0.8128$). In contrast, crabs exposed to the Low-pH treatment for 4 weeks were slower to detect prey than those in the Control treatment (repeated-measures ANOVA, $F_{1,17} = 5.268$, $p = 0.034$, Figure 2). Variation in prey detection speed among individuals was also significantly greater for crabs exposed to Low-pH conditions for 4 weeks, compared with crabs in the Control treatment (Levene's test, $W_{1,19} = 17.079$, $p < 0.001$). Individual variation in response to Low-pH waters is evident in a subset of the population. For one-third of individuals ($n = 5$ each) in each treatment with the most rapid prey detection speeds, no difference in the mean speed was detectable (repeated-measures ANOVA, $F_{1,12} = 0.084$, $p = 0.7769$). There was a significant correlation between the average antennular flicking rate for each individual and its prey detection speed 4 weeks into the pH treatments ($R = 0.561$, $F_{1,17} = 8.720$, $p = 0.008$).

Respiration rates

Oxygen consumption rates were similar between groups for crabs exposed to *in situ* conditions before the experiment (Mann–Whitney $U = 25$, $n_1 = 8$, $n_2 = 7$, $p = 0.728$; Figure 3). After 3 weeks of exposure to treatment conditions, the mean O_2 consumption rates had increased in crabs exposed to Low-pH seawater, but the difference compared with their pretreatment rates was marginally significant (Mann–Whitney $U = 13$, $n_1 = 7$, $n_2 = 9$, $p = 0.050$). Rates in the Low-pH group were significantly greater than for Control animals after 3 weeks exposure (Mann–Whitney $U = 15$, $n_1 = 8$, $n_2 = 9$, $p = 0.043$). Furthermore, there was a significant negative correlation between O_2 consumption and antennular flicking rates ($R = 0.570$, $F_{1,17} = 7.218$, $p = 0.012$). The variance in O_2 consumption among individuals did not vary among pH treatments (Levene's test, $W_{1,15} = 0.958$, $p = 0.343$).

After 8 weeks of exposure, the mean rate of O_2 consumption in the Low-pH group had returned to pre-experiment levels (Mann–Whitney $U = 56$, $n_1 = 7$, $n_2 = 12$, $p = 0.237$) and did not differ from the Control group (Mann–Whitney $U = 61$, $n_1 = 12$, $n_2 = 11$, $p = 0.758$). Respiration rates of crabs in the Control group, however, gradually decreased during the 9-week exposure period (Mann–Whitney $U = 73$, $n_1 = 8$, $n_2 = 11$, $p = 0.017$; Figure 3).

Discussion

Our results indicate that seawater acidification impairs some behaviours in *P. tanneri* that are intimately coupled to their survival. Significant reduction in the rate of antennular flicking almost certainly disrupts olfactory function that may be essential for information gathering (e.g. detecting empty shells to change or prey to eat; de la Haye *et al.*, 2011). Antennule flicking is assumed to disrupt fluid boundary layers around antennule hairs and promote transport of odour molecules to sensory cells (Reidenbach and Koehl, 2011). A significant correlation between antennular flicking rate and prey detection time, and the significant increase in time required for detecting prey in crabs under low pH conditions supports this notion. These results indicate that a reduction in the pH of deep-sea waters expected in the future may impair olfactory functions of deep-sea hermit crabs and corresponding survival skills, unless *P. tanneri* can longer term acclimatization and adaptation to these conditions.

We expected metabolic rates to be positively correlated with antennular flicking rates. In contrast, we observed that after 3 weeks immersion in low pH waters, metabolic rates had increased, but antennular flicking rates were reduced. Higher metabolic activity may instead represent the energetic costs of up-regulating important homeostatic mechanisms (i.e. acid–base balance) related to exposure to high CO_2 conditions (Pane and Barry, 2007). Or, perhaps other physiological processes such as phasic contractions of short muscles, or stereotyped impulse bursts in motor neurons (Mellon, 1997) directly related to olfactory functions are inhibited by seawater acidification and reduce antennular flicking directly (Nilsson *et al.*, 2012). A return of respiration rates to pretreatment levels after 9 weeks exposure to low pH water suggests that this population has the capacity to acclimate to a lower pH, at least in relation to metabolic rate.

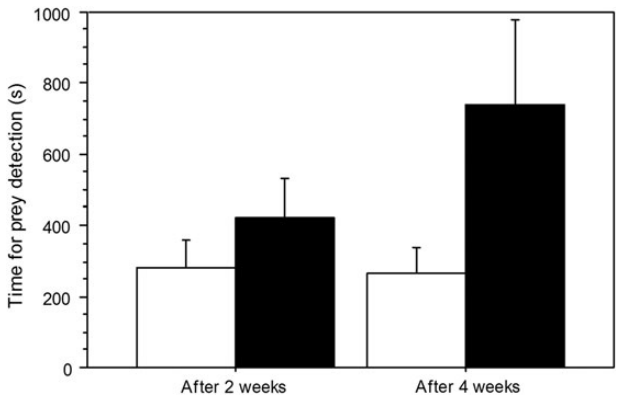

Figure 2. Time (mean ± s.e.) required for prey detection of hermit crabs (*P. tanneri*) under Low-pH (black bar) and Control (white bar) conditions. Crabs in the Low-pH treatment (pH 7.1) required more time for prey detection and had higher individual variation than crabs under Control conditions (pH 7.6) after 4-week exposure.

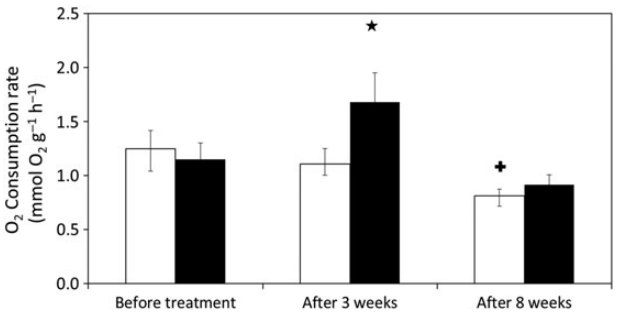

Figure 3. O_2 consumption (mean ± s.e.) of hermit crabs (*P. tanneri*) before and during exposure to Low-pH (black bar) and Control (white bar) conditions. Significant ($p < 0.05$) difference from pretreatment measurements is denoted by "plus symbol", while "asterisk" represents significant ($p < 0.05$) difference between the Low-pH and Control groups for the same period.

Hermit crabs use shells built by gastropods and are thus highly dependent on the availability of this resource (Williams and McDermott, 2004). Shells of most crabs in our experiment were considerably corroded by low pH seawater and even somewhat by control waters during the course of the experiment. The significant decrease in respiration rates of "control" crabs during the experimental time frame may be at least in part due to the observed deterioration of shell condition (Alcaraz and Kruesi, 2012). Shells become lighter due to the corrosion and so it may be easier to carry them. To this end, the ability of the snails providing shells to *P. tanneri* to survive and build carbonate shells must also be evaluated to predict the fate of deep-sea hermit crabs in future ocean chemistry.

Increased variation among individuals of *P. tanneri* in response to low pH conditions, for both antennular flicking rates and time taken for prey detection may represent a range of acclimation abilities among individuals and/or an epigenetic effect. Notably, the behaviour of the one-thirds of crabs in Low-pH treatment with the highest flicking rates did not differ from crabs in the Control group. This suggests that a large portion of the hermit crab population could acclimate to increased environmental CO_2 without a decrement in performance (i.e. survive without a fitness compromise) related to olfactory functions. Conversely, a portion of the population may be impaired to some degree, perhaps including a loss of fitness that would presumably promote adaptation favouring more tolerant genotypes. Indeed, recent reports suggest that various taxa may be able to adapt to human-induced rapid environmental changes through high individual variation in behavioural responses (Sih *et al.*, 2011, 2012; Tuomainen and Candolin, 2011). On the other hand, several studies documenting significant sensitivities of animals to ocean acidification have found no evidence for individual variation in behavioural responses to high CO_2 (e.g. Munday *et al.*, 2009; Dixson *et al.*, 2010; Cripps *et al.*, 2011; de la Haye *et al.*, 2011).

Our results showing evidence of high variation among individuals for behavioural and physiological responses to environmental hypercapnia have strong implications concerning the role of phenotypic (and presumably genetic) diversity within populations in promoting adaptation to ocean acidification. Several studies report that high individual variation in rates of development and growth in response to in low-pH exposure is linked to genetic variation (Parker *et al.*, 2011; Pistevos *et al.*, 2011; Sunday *et al.*, 2011; Kim *et al.*, 2013). We cannot confirm that tolerance or acclimation to low-pH conditions by a portion of adult hermit crabs examined is a heritable trait, as required for adaptation. Further studies on heritability of behavioural and physiological traits will shed light on understanding the adaptive capacity of deep-sea species to ocean acidification.

Acknowledgements

We thank Kurt Buck and Patrick Whaling for technical support, Peter Brewer for consultation on deep-sea carbonate chemistry, Kim Reisenbichler for technical assistance with respirometry, and Linda Kuhnz for identification of hermit crabs. This research was supported by the David and Lucile Packard Foundation, KIOST (PE99247 and PE99317), and MOF through KIMST (PM57991).

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Handling editor: Howard Browman