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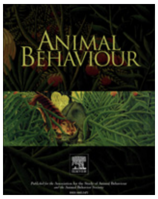

Reduced sea water pH disrupts resource assessment and decision making in the hermit crab *Pagurus bernhardus*

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The decisions that animals make are based on information gathered from their environment, and can have consequences for their fitness and survival. Such processes can be disrupted by environmental change. Hermit crabs find and select the gastropod shells they inhabit using chemical and visual cues, and tactile assessment. The choice of an optimal shell is important since it provides shelter against environmental extremes and protection against predators; inhabiting a suboptimal shell can also reduce fecundity. Hermit crabs are subject to cyclical reductions in the pH of the water in the intertidal rock pools that they inhabit, and such reductions may be further exacerbated by climate change. Reduced sea water pH, a consequence of ocean acidification and leaks from geological storage sites, has already been shown to disrupt the behaviour of marine animals. We investigated the effects of reduced sea water pH on the shell assessment and selection behaviour of the hermit crab *Pagurus bernhardus*. Under highly reduced pH conditions (pH 6.8) crabs were less likely to change from a suboptimal to an optimal shell than those in untreated sea water; those that did change shells took longer to do so. Crabs in the reduced pH treatment also showed significantly lower antennular flicking rates (the 'sniffing' response in decapods) and reduced movement. Thus, a reduction in sea water pH disrupts the resource assessment and decision-making processes of these crabs, indicating that the ability to acquire a vital resource may be influenced by both naturally occurring environmental cycles and anthropogenically induced environmental change.

The decisions animals make can have far-reaching consequences for both their fitness and survival (Dill 1987; Blumstein & Bouskila 1996; Schmidt et al. 2010). Animals continually gather and assess information about their environment, in order to make decisions such as where to look for food (Pyke et al. 1977), how to choose a potential mate (Jennions & Petrie 1997), which habitat to settle in (Johnson & Strathmann 1989), whether to hide to avoid predators (Lima & Dill 1990), or whether to enter into a fight (Arnott & Elwood 2009). The environment from which animals gather this information may be constant or variable. Some variability constitutes predictable change, like natural cycles, although these may still suspend or interfere with information-gathering activities. Environmental variability is common and animals have therefore evolved strategies to cope with such 'predictable unpredictability' (Wells 2007). Information gathering, although energetically costly, can be used to reduce ecological uncertainty; and behavioural plasticity, an evolutionary strategy that anticipates environmental variability, allows animals to respond to change on the basis of the information that they gather (Dall et al. 2005; Donaldson-Matasci et al. 2008). However, uncertainty can never be entirely eliminated and both stochastic natural events and anthropogenic effects can disrupt the environment. Information must be both acquired and processed successfully in order to be useful, and a growing number of studies have shown how changes in the environment, particularly anthropogenically induced ones, can disrupt these processes (Scott & Sloman 2004; Zala & Penn 2004; Tuomainen & Candolin 2010). Such changes can interfere with the information-gathering process itself, by compromising sensory systems, or by altering the stimulus, and this has been termed 'info-disruption' (Lürling & Scheffer 2007). Environmental changes can also affect an animal's physiology, thereby disrupting the processing of information and decision making owing to neurological disturbance (Dias-Ferreira et al. 2009; Graham et al. 2010); or they can induce metabolic stress, resulting in certain energy-demanding behaviours being allocated a lower priority in favour of maintaining homeostasis (Bernatis et al. 2007).

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Variability and disruption make decision making a more complex process for animals, where the consequences of their choices cannot be known a priori, introducing the possibility of maladaptive, as well as adaptive, responses (Dall et al. 2005; Miner et al. 2005; Schmidt et al. 2010). Many decisions, made within the context of environmental uncertainty and disruption, can involve animals in costly trade-offs that may simultaneously afford fitness benefits and incur fitness penalties (Domenici et al. 2007).

Environmental changes caused by anthropogenic effects have been shown to disrupt the information gathering and decision making of aquatic organisms. Changes in water pH, in particular, have altered the behaviour of crayfish (Allison et al. 1992), freshwater and marine molluscs (Bibby et al. 2007; Turner & Chislock 2010) and fish (Leduc et al. 2004; Munday et al. 2009; Dixson et al. 2010). In intertidal rock pools pH fluctuates naturally, along with other physicochemical characteristics (Truchot 1988). These small, intermittently isolated environments can experience enormous spatial and temporal variability in pH, salinity, temperature and oxygen concentrations, which are dependent upon weather conditions, the time of day and the abundance of resident organisms (Huggett & Griffiths 1986). The pH in rock pools can rise and fall rapidly on a diurnal basis during emersion (e.g. 9.5–6.5 pH units, Morris & Taylor 1983; 10.16–7.29 pH units, Truchot 1988), owing to algal and animal respiration. As well as undergoing natural cyclical changes in rock pools, sea water pH is predicted to fall on a global scale owing to anthropogenically induced ocean acidification (Caldeira & Wickett 2003; Raven et al. 2005). Extreme and localized high-CO_2/low-pH events could also occur as a result of leaks from sea bed carbon dioxide (CO_2) sequestration sites, proposed as a mitigating strategy for CO_2 emissions (Hawkins 2004). The average pH in rock pools is therefore likely to be reduced, and perhaps even forced below its natural limits, in the future, owing to the additive effect of ocean acidification and potential point source leaks from CO_2 storage sites. This could have biological consequences for intertidal species many of which, although resilient, are already living at the threshold of their tolerance limits (Stillman 2002; Tomanek & Helmuth 2002). Any disruption to the information-gathering and decision-making activities of intertidal animals, even over diurnal cycles, could have overall consequences at the level of population health and, if there is a differential effect among individuals, fitness consequences.

The hermit crab *Pagurus bernhardus* is a decapod crustacean (Anomura), which for most of its early adult life is commonly found in intertidal rock pools. Unlike brachyuran crabs it has an asymmetrical, membranous abdomen that is protected by the adoption of an empty gastropod shell. These gastropod shells are an important resource for hermit crabs, as they protect their soft bodies from both predation and environmental stressors (Lancaster 1988). As hermit crabs grow, they constantly upgrade to a larger shell. They acquire shells either by locating sites where there are empty shells, or by competing with each other and engaging in contest behaviour to obtain a better shell (Hazlett 1981). Hermit crabs gather information about available gastropod shells using visual cues (Elwood & Neil 1992) and through the olfactory detection of calcium ions (Mesce 1982; Gravel et al. 2004) or of dead gastropods (Rittschof et al. 1990). Like other decapod crustaceans, hermit crabs possess short antennules that are used for distance chemoreception (Snow 1975). The antennules are flicked rapidly at the onset of a stimulus (the ‘sniffing’ response in decapods) to ascertain its nature, concentration and direction (Schmitt & Ache 1979; Koehl 2006). When hermit crabs locate a suitable shell they undertake characteristic shell investigation behaviour to assess the size and quality of the prospective shelter before deciding to exchange shells (Reese 1962; Jackson & Elwood 1989). Choosing an optimal shell can have important consequences for survival, growth and fitness (Bertness 1981). Such ritual assessment and decision making in hermit crabs also extends to contest behaviour (Briffa & Elwood 2000), and, to a lesser extent, to mate choice and antipredator behaviours (Jackson & Elwood 1989; Briffa & Twyman 2011). *Pagurus bernhardus* is an excellent model organism for investigating the potential effects of reduced pH on shell investigation and chemosensory behaviour because the behavioural repertoire used for shell selection, under normal conditions, is already well understood (Jackson & Elwood 1989), such that any changes caused by low pH may be readily identified, and its antennular flicking is a tractable measure of chemoresponsiveness.

In this study, we determined the effects of exposure to reduced sea water pH on the ability of *P. bernhardus* to detect empty gastropod shells, either visually or chemically, and on its subsequent shell investigation and shell choice behaviour. One possibility is that any apparent reduction in the ability to detect shells, and in shell investigation, could be caused by overall metabolic depression and a related lack of motivation to search for new shells, as a result of exposure to reduced pH. In this case we would expect the lower pH to cause a reduction in overall activity rates, which, as well as indicating a lack of olfactory stimulation, can also be an indicator of physiological condition. On the other hand, if the effects on the specific chemoresponsive behaviour (antennular flicking) and shell choice behaviour were more marked than the effects on nonspecific activity rates, this would indicate either greater flexibility in these particular behaviours or the possibility of a specific effect upon them.

METHODS

Study Organisms

Hermit crabs, *P. bernhardus*, were collected by hand from midshore rock pools at Hannafore Point, Looe, Cornwall, U.K. (50.20°N, 04.27°W), February to March 2009. Crab mass was standardized as much as possible (mean $= 1.2 \pm 0.7$ g). Only crabs inhabiting *Littorina littorea* shells were collected, as this is the preferred shell species for crabs of this size (Briffa & Elwood 2007). In the laboratory, individuals were kept in holding aquaria (80 litres) supplied with aerated, filtered sea water (salinity $= 34$). Approximately 50 hermit crabs were held in each aquarium and were provided with numerous refuges to limit potentially harmful agonistic interactions and cannibalism. All aquaria were maintained under conditions of natural light and at a temperature of 15 °C. At least 1 week was allowed to elapse between collection and the start of the experiment to acclimate the hermit crabs to laboratory conditions. During the holding period, crabs were fed with the white fish coley, *Pollachius virens*. Two days before the start of the experiment crabs were randomly selected and placed in individual 1-litre aquaria. To standardize hunger levels, all crabs were food deprived during this period, and 24 h before the experiment the hermit crabs were carefully excised from their original shells using a bench vice, and their sex determined. Only males with a full complement of undamaged limbs and free from obvious parasites were used, to control for intersexual differences in shell selection behaviour. Each crab was presented with an empty, suboptimal shell (50% of the mass of an optimal shell, determined from a previous shell selection experiment by Briffa & Elwood 2007), and allowed to recover for 24 h before sea water treatments commenced.

Experimental Design

We used a repeated measures design where crabs were divided into two Groups (A and B). In the first part of the experiment both groups were kept in untreated sea water ($pH_{NBS} = 8.2$) for 5 days and then underwent behavioural trials in which they were offered an optimal shell and their shell investigation behaviour was