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Review

High CO_2 and marine animal behaviour: Potential mechanisms and ecological consequences

Mark Briffa[a,*], Kate de la Haye[a], Philip L. Munday[b]

[a] School of Marine Science and Engineering, Plymouth University, Drake Circus, Plymouth PL4 8AA, UK
[b] ARC Centre of Excellence for Coral Reef Studies, and School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia

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ABSTRACT

Exposure to pollution and environmental change can alter the behaviour of aquatic animals and here we review recent evidence that exposure to elevated CO_2 and reduced sea water pH alters the behaviour of tropical reef fish and hermit crabs. Three main routes through which behaviour might be altered are discussed; elevated metabolic load, 'info-disruption' and avoidance behaviour away from polluted locations. There is clear experimental evidence that exposure to high CO_2 disrupts the ability to find settlement sites and shelters, the ability to detect predators and the ability to detect prey and food. In marine vertebrates and marine crustaceans behavioural change appears to occur via info-disruption. In hermit crabs and other crustaceans impairment of performance capacities might also play a role. We discuss the implications for such behavioural changes in terms of potential impacts at the levels of population health and ecosystem services, and consider future directions for research.

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1. Pollution and behaviour

Elevated atmospheric carbon dioxide (CO_2) concentration leads to increased CO_2 absorption by the sea, causing a suite of changes in sea water carbonate chemistry. Increased CO_2 absorption also leads to reduced sea water pH and therefore the process is frequently referred to as 'ocean acidification' (OA). In addition to changes resulting from increased atmospheric ambient CO_2, there is the potential for very severe localised effects on sea water chemistry as a result of carbon dioxide leaks from Carbon Capture Storage (CCS) sites, which have been proposed as a mitigating strategy for CO_2 emissions (Hawkins, 2004). Such changes in sea water chemistry are one form of anthropogenic pollution of marine environments. The potential for pollution to influence animal behaviour is gaining increasing attention (e.g. Sih et al., 2011; Tuomainen and Candolin, 2011; Zala and Penn, 2004) and in aquatic environments, pollution has the potential to affect animal behaviour in three ways. First, pollution might disrupt proximate causal mechanisms, such as metabolic processes, that determine the rates at which behaviour can be performed. This is particularly likely in the case of demanding behaviours such as foraging or aggression, where the link between metabolism and performance capacities has been well established (see Briffa and Sneddon, 2007 for a review). The potential for pollution to disrupt behaviour in this way is well illustrated by studies on the effects of heavy metal and polycyclic hydro-carbon (PAH) pollutants. In arthropods copper is an essential constituent of the respiratory pigment haemocyanin, but when present at elevated levels in the environment, it can become toxic (e.g. Briffa, 1976). In the shore crab *Carcinus maenas*, copper exposure leads to reduced heartbeat rate (Lundebye and Depledge, 1998a) and exposure to copper might therefore disrupt the ability to perform activities that require a high circulation rate, such as aggression (Rovero et al., 2000). Indeed, exposure to another pollutant, pyrene (a by-product produced during the incomplete combustion of petrochemicals) has been shown not only to impair the metabolism and immune function of *C. maenas* but also to alter their usual agonistic behaviour (Dissanayake et al., 2009). In studies of rainbow trout, *Oncorhynchus mykiss*, exposure to pollution also changes aggressive behaviour, resulting in disruption to the structure of dominance hierarchies (Sloman et al., 2003). In this study it was suggested that while cadmium exposure might have metabolic consequences, it could also disrupt social behaviour by impairing the perceptive and cognitive abilities of the fish. Thus, a second reason why the behaviour of animals in polluted environments might change is that the ability to gather information ('perception') and to assess that information and then make decisions ('cognition') might be disrupted. Information gathering and decision-making are key behavioural processes, which have been investigated at length in marine animals such as hermit crabs (Elwood and Briffa, 2001). The ability of anthropogenic disturbances to disrupt these processes has been termed 'info-disruption' (Lürling and Scheffer, 2007). The third way in which pollution might change behaviour

* Corresponding author.
E-mail address: mark.briffa@plymouth.ac.uk (M. Briffa).

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patterns is that animals might be able to detect and avoid polluted locations (Pörtner and Peck, 2011).

Studies of social structures and aggression (e.g. Sloman et al., 2003; Dissanayake et al., 2009; Sopinka et al., 2010), as well as other behavioural processes such as mating (Krång and Ekerholm, 2006; Ward et al., 2008), demonstrate the potential for exposure to pollution to alter the behaviour of aquatic animals. Here, we review the current evidence for behavioural disruption as a result of exposure to sea water that has undergone elevated CO_2 absorption. We first discuss the potential causal pathways linking elevated CO_2 to disrupted behaviour. In the following sections we then review the empirical evidence for the presence of behavioural disruption due to elevated CO_2 focussing on case studies of tropical coral reef fishes (e.g. the clownfish, *Amphiprion percula*, damselfish, *Pomacentrus wardi* and *Pomacentrus moluccensis* and the brown dottyback, *Pseudochromis fuscus*) and common European hermit crabs (*Pagurus bernhardus*). We then discuss the links between disrupted behaviour at the level of the individual and potential cascading effects at the population and ecosystem levels. In comparison to studies of other forms of pollution, interest in the potential effects of OA is relatively recent. While initial studies tended to focus on the potential effects of reduced pH *per se*, more recent studies indicate that it is exposure to high CO_2 (hypercapnia), and its effects, that may be responsible for the majority of observed disruptions to the physiology and behaviour of marine animals (Pörtner et al., 2004; Melzner et al., 2009; Nilsson et al., 2012). It is clear for example, that elevated CO_2 disrupts the ability of some marine invertebrates to maintain their acid–base balance (Pörtner et al., 2004; Spicer et al., 2006), and this is one physiological mechanism that could have downstream effects on behaviour. Of course, behavioural processes may be altered by effects on multiple interacting pathways, producing changes that are not readily predictable. On the basis of the experiments reviewed below, however, it is clear that OA and therefore leakage from proposed CCS schemes, can change the behaviour of marine animals.

2. Potential mechanisms linking elevated CO_2 to behavioural change

In the case of marine crustaceans such as *C. maenas* the link between exposure to pollutants, such as heavy metals and PAHs, and impaired behaviour seems clear: significant physiological costs allocated to coping with pollutants (Lundebye and Depledge, 1998b; Dissanayake et al., 2008) reduce the energy available (i.e. metabolic scope, MS, is reduced) for meeting other demands and thus behavioural performance capacities are reduced (Dissanayake et al., 2010). For what reasons might we expect exposure to elevated CO_2 to exert similar effects in marine animals? First, there is now clear evidence for the presence of significant developmental and physiological costs with exposure to elevated CO_2 in some invertebrate species (Pörtner et al., 2004; Orr et al., 2005). As noted above, under conditions of high CO_2 marine animals might experience an increased metabolic load due to the elevated costs of maintaining acid–base balance (Pörtner et al., 2004; Spicer et al., 2006). Thus, as in the case for exposure to other pollutants, changes in underlying physiological condition as a result of exposure to high CO_2 might constrain the ability to perform key behaviours, such as swimming (Dissanayake and Ishimatsu, 2011).

In addition to reduced metabolic scope, a second pathway through which high CO_2, and possibly low pH, might disrupt behaviour is through 'info-disruption', that is, impairment of the ability to gather and assess information and therefore to make decisions. There are several routes through which exposure to high CO_2 could lead to info-disruption. One possibility is that chemoreception, the ability to detect chemical cues, is impaired. Marine animals depend on the detection of chemical cues in order to obtain information about their environment (e.g. Wisenden, 2000; Hay, 2009; Ferrari et al., 2010; Breithaupt and Thiel, 2011) and any change to sea water chemistry could therefore interfere with the detection or recognition of these cues. The potential for reduced pH to disrupt this process of 'chemoreception' was initially discovered in freshwater fish (Hara, 1976) and crayfish (Tierney and Atema , 1986,1987; Allison et al., 1992). In freshwater systems, pH may be markedly reduced by acid rain and these studies demonstrated how the ability to detect amino-acids associated with food odours was reduced under such conditions. Although marine animals are adapted for a very different chemical environment in comparison with freshwater species, the basis of chemoreception is similar. In both cases detection of a protein based chemical cue, for example, is dependent on an odour molecule binding with a receptor site on the surface of chemoreceptive cells of the animal's chemoreceptive organs (Tierney and Atema, 1987). In freshwater examples, reduced pH-induced changes to the charge distribution on these receptor sites might explain why individuals under conditions of reduced pH show reduced chemoresponsiveness (Tierney and Atema, 1987). Although these studies investigated acidification *per se* (as a result of acid rain) rather than hypercapnia, similar effects in marine species might result from a reduction in sea water pH. In addition to changing the charge distribution at odour molecule receptor sites, reduced pH could disrupt chemoresponsive behaviour by causing a change in the ionic state of the odour molecules themselves (Hara, 1976; Brown et al., 2002; Leduc et al., 2004), making them un-recognizable or preventing binding with receptor sites. A more severe cause of info-disruption might be physical damage to information gathering organs. In calcifying animals, for example, elevated CO_2 can lead to problems in maintaining the structure of the exoskeleton, eventually leading to a degree of dissolution (Spicer et al., 2006), such that there may be damage to delicate sensory structures. In cases where this possibility has been investigated directly, however, (Munday et al., 2009 nasal cavity gross structure in reef fish; de la Haye et al., 2012 antennules in hermit crabs; Simpson et al., 2011, otoliths in reef fish ears) there has been no evidence that sensory structures are damaged by exposure to high CO_2 conditions. On the other hand, recent studies on fish indicate that a change to sea water chemistry might damage the neural mechanisms involved in information processing (Domenici et al., 2012; Nilsson et al., 2012). Thus, rather than impairing detection, high CO_2 could impair cognition and through this route affect a wide range of sensory functions and behaviours.

A third proposed route through which high CO_2 might cause disruption to normal behaviour, is that animals might show avoidance of localised pollution (Pörtner and Peck, 2011). Thus, elevated CO_2 and other forms of pollution might alter the normal movement patterns and distribution of marine animals. Elevated CO_2 could therefore impact behaviour via three distinct routes: disruption to an animal's underlying physiological state could lead to constraints on the ability to perform behaviours or to changes in motivation; the information received by the animal, or the animal's ability to capture, process and respond to information is impaired by elevated CO_2 (info-disruption); finally, reduced pH might elicit avoidance behaviour in animals, affecting their distribution patterns. See Table 1 for a summary of these proposed mechanisms.

The mechanisms discussed above should not be regarded as mutually exclusive or isolated from one another. For example, the presence of impaired performance capacities or of info-disruption might reduce the scope for avoidance behaviour. An illustration of the potential for behaviour to be disrupted by an interaction between different causal mechanisms that are each disrupted by elevated CO_2 is provided by a study on the intertidal gastropod *Littorina littorea* (Bibby et al., 2007). Individuals

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