INTRODUCTION

Acidification of the world’s oceans by the absorption of anthropogenic CO2 is causing so much concern that it is gaining recognition alongside climate change as ‘the other CO2 problem’ (Doney et al. 2009). Global atmospheric pCO2 levels have increased from 0.03 to 0.04 kPa since pre-industrial times and are predicted to reach ~0.08 kPa by 2100 (‘business-as-usual’ CO2 emission scenario, Houghton et al. 2001). More than a third of the atmospheric CO2 emitted into the atmosphere since the beginning of the industrial revolution has been absorbed by the oceans, resulting in an alteration in the seawater carbonate system to give a 30% increase in H⁺ concentrations (0.1 pH unit) and a 16% reduction in carbonate ion concentrations (Feely et al. 2004, Fabry et al. 2008). As ocean acidification is happening at a rate that outstrips the neutralising action of sedimentary antacids, it is predicted that the continued release of fossil-fuel CO2 into the atmosphere will reduce ocean pH levels from present day levels of 8.1 to 7.8–7.7 by the end of the century (Orr et al. 2005), and to pH 7.4 by 2300 if atmospheric CO2 reaches 0.20 kPa (Caldeira & Wickett 2003). Critically, pH levels will be lower than those experienced for the past 25 million yr (Royal Society Report 2005, Widdicombe & Spicer 2008).

The biological effects of ocean acidification are still far from clear, although interest in this area has intensified considerably over the past 7 yr (Pörtner et al. 2004, Fabry et al. 2008, Pörtner 2008, Przeslawski et al. 2008, Doney et al. 2009). Over this time period, there
has been a tendency to concentrate on marine taxa considered to be the most vulnerable to ocean acidification, such as cnidarians, echinoderms and molluscs. These taxonomic groups have received the most attention because calcification of the external shells and skeletons is influenced by the changes in seawater pCO$_2$, pH and [CO$_3^{2-}$] associated with ocean acidification. In extreme cases, for instance, elevated seawater CO$_2$ can cause dissolution of the calcified skeleton and reduce calcification rates (e.g. Gattuso et al. 1998, Langdon et al. 2000, Kleypas et al. 2006, Gazeau et al. 2007). Physiological studies have also revealed that echinoderms and bivalve molluscs are likely to be the most vulnerable to ocean acidification because they are poor iono-regulators and show little ability to buffer the acidifying effects of elevated CO$_2$ in their body compartments (Fabry et al. 2008, Widdicombe & Spicer 2008, Doney et al. 2009, Melzner et al. 2009, Dupont et al. 2010). The resulting consequences can be far reaching as acidification of body compartments can lead to metabolic depression (Michaelidis et al. 2005, Miles et al. 2007, Rosa & Seibel 2008), a reduction in energy stores (Langenbuch & Pörtnner 2002, 2003) and a reduction in growth rate (Michaelidis et al. 2005, Beniash et al. 2010). Physiological studies can therefore be used to explain species-related differences in sensitivity, which, in turn, can be used to predict changes in individual performance and survival. Consequently, physiological changes have been used in the recent past to inform on the ecological effects of ocean acidification (Fabry et al. 2008, Guinotte & Fabry 2008, Widdicombe & Spicer 2008, Dupont et al. 2010). Over the past 7 yr there has been a concerted effort to switch attention from short-term acute exposures (hours to days) to extremely high pCO$_2$ levels (hypercapnia) to more relevant pCO$_2$ over longer time intervals, such as medium-term (weeks) to long-term exposure (months) (Fabry et al. 2008, Widdicombe & Spicer 2008, Doney et al. 2009). There has also been a move towards studies based on community mesocosms in order to examine changes in biodiversity and community structure (Widdicombe et al. 2009, Hale et al. 2011). In addition, there is a growing realisation that concomitant changes in other environmental variables, such as temperature, salinity and oxygen, may also modify responses to ocean acidification and further decrease chances of survival (Fabry et al. 2008, Widdicombe & Spicer 2008, Findlay et al. 2010a,b). Finally, there has been an increasing interest in the survival of early developmental and reproductive stages, which are likely to be the most vulnerable to ocean acidification (Dupont et al. 2008, 2010, Kurihara 2008).

Collectively, these approaches have demonstrated that the ability to tolerate ocean acidification is species specific and varies within phyla and between closely related species (Doney et al. 2009, Melzner et al. 2009, Hale et al. 2011). As we learn more about the long-term effects of ocean acidification on the physiology and ecology of marine invertebrates, it is becoming apparent that even those species generally tolerant of ocean acidification are under threat. Medium- to long-term compensation for projected ocean acidification conditions could prove to be energetically costly. Examples already exist in the literature to indicate that energy can be diverted away from key biological processes such as growth and reproduction towards compensatory responses (e.g. Wood et al. 2008, Beniash et al. 2010). On the other hand, certain species may be more resilient than once thought because they can acclimatise or adapt to the changes. Clearly, we need to examine the effects of ocean acidification on a wider range of species from different taxa to get a better idea of the possible effects of the projected climate change conditions on marine species, communities and ecosystems. Valuable lessons could be learned from taxa that have been largely overlooked, especially those that are considered to be tolerant of ocean acidification, such as crustaceans.

The effects of oceanic acidification on marine crustaceans have received some attention, however, the studies are disparate and have been conducted on widely divergent species for varying lengths of time at different pCO$_2$ levels. Our general lack of knowledge on the potential effects of ocean acidification on marine crustaceans is surprising because most crustaceans are characterised by a mineralised chitinous exoskeleton, which could be affected by changes in seawater carbonate chemistry. Crustaceans are also ecologically and economically important. In addition, there is a wealth of background physiological information that can be used to explain differing sensitivities to ocean acidification. If crustacean species are adversely affected by ocean acidification, then this could have far-reaching ecological consequences, as crustaceans are primary and secondary consumers and an important food source for higher trophic levels. For instance, crustacean species form the bulk of the zooplankton and can be present in vast numbers, either as pelagic larvae or as adults. Total biomass can reach impressive levels, as shown in the Southern Ocean where Antarctic krill *Euphausia superba* reach a total biomass of 133 million tonnes at any one time (Atkinson et al. 2009). Any adverse effects could also have an impact on the shellfish industry, as several decapod species (lobsters, crabs, prawns and shrimps) can be cultured or harvested for food or bait. Shellfish culture, which includes both crustaceans and bivalves, has increased in importance in recent years, reaching 20% of the global seafood production (T. Pickerell, Shellfish Association of Great Britain, pers. comm.).
Most of the 68,000 extant species of Crustacea described to date are marine (Martin & Davis 2001, 2006). While some groups are exclusively marine (e.g. cirripeds, euphausiids, stomapods) and occupy every available niche in the ocean, others are primarily marine, but have brackish, freshwater and semi-terrestrial/terrestrial representatives (e.g. ostracods, copepods, isopods, amphipods, decapods). Subsequently, crustaceans occupy a range of aquatic habitats that experience differing degrees of environmental variability. Those occupying deep oceans and high latitudes come from relatively stable environments where physical factors show little variation over temporal and spatial scales. Other environments, such as the intertidal zone and estuaries, can experience wide and rapidly changing fluctuations in physical factors in response to diurnal changes in tidal height. In estuarine environments, seasonal changes in physical variables are affected by changes in the inputs of freshwater and nutrients. Consequently, crustaceans are unusual when compared with other marine taxa. This is because they show a wide variety of responses to salinity change, from those that can regulate against external changes to those that simply conform. Studies on crustaceans can therefore provide researchers with an ideal opportunity to examine the relationship between environmental variability and the capacity to tolerate ocean acidification, which has recently been debated in the literature (Fabry et al. 2008, Widdicombe & Spicer 2008).

The purpose of the current review is to bring together, for the first time, all of the ocean acidification studies that have been carried out on crustaceans to date. The review will follow the development of the field from early physiological studies on the effects of hypercapnia to the effects of long-term exposure to more relevant pCO2 levels on individual performance and fitness. The physiological data will be used to investigate the presence of any emerging patterns or trends that may explain why certain groups of crustaceans are more vulnerable to ocean acidification than others. The subsequent ecological repercussions will be reviewed by summarising our current understanding of the following: the possible energetic implications of medium-term exposure to relevant pCO2 levels, the potential impacts on calcification rates and growth in crustaceans, as well as a summary of the latest observations on the effects of ocean acidification on development rates and larval survival. As such, the current review will use physiological and ecologically relevant responses to give an overall view on the biological effects of ocean acidification on crustaceans. This information will be used to identify areas for future research so that we can make a more informed assessment on the future prospects for marine crustaceans in a high CO2 world.

**PHYSIOLOGICAL RESPONSES TO OCEAN ACIDIFICATION**

The most immediate responses to ocean acidification in marine crustaceans are best described at the individual level by physiological adjustments to changes in seawater carbonate chemistry. As the majority of crustaceans are committed water-breathers, they are in close contact with their external environment via the gills or equivalent structures, which are specialised for respiratory gas and ion exchange (Taylor & Taylor 1992). When carbonate chemistry of the seawater changes during ocean acidification, CO2 excretion across the gills is compromised, causing an increase in CO2 in the haemolymph (extracellular compartment). Subsequent changes in haemolymph pH are buffered to various extents by the mechanisms described in the following subsection. Such adjustments are important because they maintain the acid–base equilibria of the body fluids within the limits needed for protein function. This is particularly true for the intracellular compartment, where changes in pH are tightly controlled. A rise in intracellular [H+] can disrupt key biological processes such as metabolism, protein synthesis, ionic-regulation and cell volume control (Gaillard & Malan 1983, Wheatly & Henry 1992, Whiteley 1999). Although pH disruptions can be tolerated in the haemolymph or extracellular compartment to some extent for short periods (hours), haemolymph pH regulation is important to maintain oxygen supply. Increasing [H+] will decrease the oxygen affinity of the respiratory pigment, reducing oxygen delivery to the tissues (Taylor & Whiteley 1989, Whiteley & Taylor 1992). Disruptions to extra- and intracellular acid–base balance can, therefore, have far-reaching consequences by compromising survival and adversely effecting ecologically relevant factors such as metabolism and growth.

**Short-term acute exposure to hypercapnia**

Most of what we currently understand about the physiological mechanisms involved in the compensation of acid–base imbalances comes from laboratory-based studies on decapod crustaceans (prawns, lobsters, portunid and xanthid crabs) exposed to acute elevations in pCO2 (hypercapnia). Although the CO2 levels investigated during short-term hypercapnia are much higher than the levels projected for future climate change scenarios, these studies are invaluable because they provide a mechanistic basis for understanding differences in the sensitivity of marine invertebrate taxa to ocean acidification (Fabry et al. 2008, Förtner 2008, Widdicombe & Spicer 2008, Melzner et al. 2009, Hale et al. 2011). Most importantly, the short-
term exposure of crabs to either hypercapnia or external changes in salinity has demonstrated that acid–base balance is closely associated with ionic-regulation because both homeostatic processes share the same mechanisms (Truchot 1975, 1981, 1992, Cameron 1978, Henry & Cameron 1982, Cameron & Iwama 1987, Whiteley 1999, Whiteley et al. 2001). Closer inspection of the mechanisms involved has revealed that pH adjustments in the haemolymph are buffered by haemolymph proteins (mainly haemocyanin) and bicarbonate ions. However, pH adjustments are dominated by electroneutral ion exchange across the gill epithelia, as the majority of buffer HCO$_3^-$ comes from the external seawater (93%) and the remainder (7%) comes from internal stores (Cameron 1985). Moreover, crustacean species that are more tolerant to hypercapnia maintain a higher haemolymph HCO$_3^-$ (Pörtner et al. 2004, Melzner et al. 2009), although HCO$_3^-$ levels do not generally exceed values $>$50 mmol l$^{-1}$ (Cameron & Iwama 1987). During electroneutral ion exchange, inward HCO$_3^-$ from the seawater is exchanged for Cl$^-$ after the catalysed hydration of CO$_2$ by carbonic anhydrase, and outward H$^+$ is exchanged for Na$^+$ (Taylor & Taylor 1992, Wheatly & Henry 1992, Whiteley 1999). These ion exchanges are driven by a basolateral Na$^+$/K$^+$-ATPase (Towle & Kays 1986, Taylor & Taylor 1992) and, possibly, an apical H$^+$-ATPase (Onken & Putzenlechner 1995, Freire et al. 2008). Consequently, environmental disruption of haemolymph acid–base status is more likely to be compensated in strong ionic- and osmoregulators, where ion exchange mechanisms are well developed. This relationship could well explain why freshwater crustaceans, which are strong ionic- and osmoregulators, can survive considerable acidification of their freshwater habitats (Abramsson 1972, McMahon & Stuart 1989, Felten et al. 2008, Weber & Pirow 2009). Likewise, strong ionic- and osmoregulators are likely to be less vulnerable to ocean acidification, because they possess the mechanisms that enable them to compensate for haemolymph acid–base disturbances, at least in the shorter term.

**Medium-term exposure to relevant CO$_2$ levels**

Exposure to smaller increases in seawater CO$_2$ (i.e. 0.10 to 0.20 kPa) over longer time intervals of weeks to months is more relevant to the potential changes that could occur as a result of ocean acidification. To date medium-term laboratory-based physiological studies in adult crustaceans have concentrated on alterations in compensatory capacities over time. The information available, however, is limited and can be traced back to a handful of studies that have either examined acid–base adjustments or calcification rates. Overall, it appears that medium-term exposure to pCO$_2$ levels more representative of ocean acidification has the potential to adversely affect growth and reproduction by diverting energy towards the maintenance of effective compensatory responses.

Acid–base compensation and energetic repercussions

Only 3 studies have examined the ability of crustaceans to adjust internal acid–base imbalances during medium-term exposure to projected pCO$_2$ levels. In the strong ionic-regulating prawn species *Palaemon elegans* and *P. serratus*, complete compensation for a pCO$_2$ of 0.30 kPa was observed after 30 d of exposure (Dissanayake et al. 2010). However, ion homeostasis was maintained at the expense of acid–base balance. Two species of crabs, Necora puber and Cancer magister, which are relatively poor ionic-regulators, were also able to compensate haemolymph acid–base disturbances within 24 h when exposed to CO$_2$ at 0.10 to 0.20 kPa (Pane & Barry 2007, Spicer et al. 2007). Compensation in all 4 species was achieved by an elevation in haemolymph [HCO$_3^-$]. Continued exposure to the same pCO$_2$ level in *N. puber* had a detrimental effect, as bicarbonate buffering started to fail after 16 d when [HCO$_3^-$] reached 27 mmol l$^{-1}$ (Spicer et al. 2007). However, haemolymph [HCO$_3^-$] was found to be much lower after 30 d at the same pCO$_2$ in a separate study (Small et al. 2010). Exposure to an even higher pCO$_2$ level of 2 kPa (pH of 6.05) limited survival to between 4 and 5 d, because haemolymph pH fell despite a huge increase in haemolymph buffer base up to 55 mmol l$^{-1}$ (Spicer et al. 2007). This bicarbonate value is similar to the maximum value obtained by Cameron & Iwama (1987) for the blue crab *Callinectes sapidus* during hypercapnia. Both observations support the existence of a threshold [HCO$_3^-$] in the haemolymph of approximately 50 mmol l$^{-1}$. The inability to increase [HCO$_3^-$] beyond this level is thought to be a compromise between acid–base balance and ionic-regulation, although it is also possible that the medium-term adjustments are metabolically expensive as suggested by Pörtner et al. (2004) for other invertebrate species.

Acid–base adjustments made by crustaceans are likely to be metabolically expensive over weeks to months, due to the dependence on HCO$_3^-$ uptake from the seawater via electroneutral ion exchange. Electroneutral exchange of HCO$_3^-$ for Cl$^-$ and H$^+$ for Na$^+$ is, in turn, dependent on the presence of ion gradients across transport epithelia that are maintained by active ion-transporting pumps, Na$^+$/K$^+$- and H$^+$-ATPases (Cameron & Iwama 1987, Pörtner et al. 2004, Santos et al. 2007). The actual costs associated with active ion
transport activity range from 2.8 to 40% of total energy expenditure, indicating a considerable cost to the individual (Pannevis & Houlihan 1992, Leong & Manahan 1997). If the costs associated with the acid–base balance are indeed significant, then crustaceans that are good compensators could be adversely affected during ocean acidification. Either the costs will be limiting and restrict homeostatic processes or energy will be diverted away from other energy-demanding processes. In both situations, individual performance will be affected. Even though the energetic consequences of ocean acidification are unknown, some indication of the possible effects on performance can be obtained from experiments in which crustaceans are acclimated to various salinities. For instance, it is well known that the maintenance of ion gradients between the extracellular fluid and the external medium is energetically costly, especially during hypo- and hyper-osmoregulation (Gilles 1983, Moreira et al. 1983, McNamara & Moreira 1987, Pèqueux 1995, Freire et al. 2008). The increase in energetic costs associated with ionic-regulation has recently been used to explain differences in protein synthesis rates in the tropical prawn Macrobrachium rosenbergii (Intanai et al. 2009). In M. rosenbergii whole animal fractional rates of protein synthesis were highest at an iso-osmotic salinity of 14 psu, when the prawns were expending the minimal amount of energy on ionic- and osmoregulation (Wang et al. 2004, Intanai et al. 2009). As protein synthesis rates are a major determinant of growth, these observations suggest that growth was compromised during hypo-and hyper-osmoregulation. Whether ocean acidification would have a similar effect on protein synthesis rates is not yet known.

Given that the energetic costs of acid–base regulation could be fairly substantial, it is also possible that the associated costs themselves could decrease during ocean acidification to reduce ATP demand. Such a response has been observed in the musculature of the intertidal polychaete Sipunculus nudus during hypercapnia (Pörtner et al. 2000). In this species, intracellular pH is protected during an extracellular acidosis by an increase in the importance of Na+-dependent Cl-/HCO₃⁻ exchange for H⁺ transport over Na⁺/H⁺, Na⁺/K⁺-ATPase, and possibly H⁺-ATPase activity. The benefit here is the shift in ionic-transporting mechanisms from those with higher to lower ATP demands. An extracellular acidosis in S. nudus was accompanied by a decrease in metabolic rate, suggesting that a decrease in the energetic demands of acid–base regulation has an effective energy-saving role (Pörtner et al. 1998, 2000). Whether this strategy exists in crustaceans exposed to more moderate increases in pCO₂ is not known.

Calcification rates

Currently it is relatively unclear whether the net calcification rate (balance between rates of calcification and dissolution) of the chitinous-mineralised crustacean exoskeleton will be adversely affected by ocean acidification. Calcification processes in crustaceans are likely to be less vulnerable to ocean acidification than those present in echinoderms or molluscs, because exoskeletal CaCO₃ is mostly in the more stable form of calcite rather than the more soluble aragonite (Boßelmann et al. 2007, Neues et al. 2007). In addition, calcification processes are well removed from external changes in seawater carbonate chemistry and are known to depend on HCO₃⁻ rather than on CO₃²⁻ (Cameron 1985). The crustacean exoskeleton also contains amorphous calcium carbonate, which is highly soluble and acts as a transient source of Ca²⁺ (Boßelmann et al. 2007, Neues et al. 2007). It is tempting to speculate that amorphous CaCO₃ may also act as a source of HCO₃⁻ for acid–base homeostasis. Interestingly, the proportion of amorphous calcium salts in the exoskeleton varies between species and depends on lifestyle (Neues et al. 2007). It may therefore influence compensatory capacities by providing a labile source of HCO₃⁻. Currently, it is not known how these various forms of CaCO₃ are affected by ocean acidification. However, the formation of CaCO₃ in the crustacean exoskeleton is thought to depend on the maintenance of an alkaline pH in the exoskeletal compartment, which is reported to be 0.3 pH units higher than that in the haemolymph (Wood & Cameron 1985).

Despite the lack of information on calcification processes in crustaceans, ocean acidification has the potential to influence calcification rates in 2 ways. First, ocean acidification could influence precipitation of CaCO₃ in the exoskeleton by reducing the alkaline pH in the exoskeletal compartment (Wood & Cameron 1985). Second, ocean acidification could interfere with post-moult calcification of the new exoskeleton, which is dependent on a large uptake of Ca²⁺ and HCO₃⁻ across the gills from the surrounding seawater (Neufield & Cameron 1992, Wheatly 1997). The influx of Ca²⁺ and HCO₃⁻ is particularly sensitive to an increase in external [H⁺] as it reduces branchial HCO₃⁻ uptake (Cameron 1985, Cameron & Wood 1985). This suggests that the reductions in seawater pH associated with ocean acidification could potentially interfere with post-moult calcification. A similar response has been observed in the blue crab Callinectes sapidus during hypercapnia. In this species, post-moult calcification, which normally takes 14 d, took twice as long, as the HCO₃⁻ necessary for calcification was obtained from metabolic CO₂ (Cameron 1985). Any delay in the post-moult calcification process could be fatal, as crus-
taceans are particularly vulnerable to predation during this period. Their exoskeletons are soft, and the newly moulted crustaceans are unable to move or defend themselves. As a consequence, ocean acidification has the potential to increase mortality rates indirectly by delaying the calcification process during molting.

Despite the potential for adverse effects on calcification rates, medium-term exposure to moderate elevations in seawater CO₂ indicates that the calcified structures in crustaceans (exoskeleton and the barnacle shell wall plates) are well protected from ocean acidification. In all crustacean species studied to date, calcification rates either remain the same or increase after a period of CO₂ exposure (Wickins 1984, Findlay et al. 2009, McDonald et al. 2009, Ries et al. 2009). An increase in calcium content was first observed in the exoskeleton of Penaeus monodon after 36 d of exposure to a decrease in seawater pH of 7.9 to 6.4 pH units (Wickins 1984). A similar response was observed in the blue crab Callinectes sapidus, the king prawn Penaeus plebejus and the lobster Homarus americanus (Ries et al. 2009). All 3 species were exposed to seawater equilibrated with pCO₂ levels that were 2, 3 and 10 times higher than pre-industrial levels (0.06 ± 0.01, 0.09 ± 0.01 and 0.29 ± 0.05 kPa, respectively) for 60 d, which is nearly twice the exposure period experienced by P. monodon in the earlier study by Wickins (1984). Such a response may reflect the ability to effectively maintain elevated pH levels at the site of calcification. It may also demonstrate that the outer organic layer, or epicuticle, acts as an effective barrier between the mineralised exoskeleton and the seawater (Ries et al. 2009). In contrast, long-term exposure to a pCO₂ of 0.01 kPa for 30 wk resulted in morphological damage in the marine shrimp P. pacificus, due to shortening of the second antennae (Kurihara et al. 2008). The authors attributed this damage to the dissolution of CaCO₃ stores by the ensuing disruptions to acid–base homeostasis, which are more likely to occur in the long term.

Recent studies on 2 species of intertidal barnacles have revealed differences in net calcification rates during elevated pCO₂. In the tropical barnacle Amphibalanus amphitrite, an increase in the calcification rate was implied by the observed increase in basal shell diameter after 11 wk at pH 7.4, which required greater force to cause shell breakage (McDonald et al. 2009). Compensatory responses, however, were localised, as the central wall plates succumbed to dissolution at pH 7.4 and were weaker than individuals held at pH 8.1. This observation suggested that individuals held at pH 7.4 would be more vulnerable to predation. In contrast, the maintenance of mineral content in the shells of the cold-temperate/boreal barnacle species Semibalanus balanoides after 20 d at pH 7.3 indicated an ability to compensate for shell dissolution in seawater saturated with aragonite and calcite, but an inability to enhance calcification rates (Findlay et al. 2010b). Given that the growth rates of S. balanoides were slower at pH 7.3 than at pH 8.1, Findlay et al. (2010b) concluded that calcification of the shell under acidifying conditions was energetically demanding, resulting in the reallocation of resources, which compromised individual fitness. Clearly, crustaceans show some ability to compensate net calcification rates for medium-term exposure at relevant pCO₂. However, a few detrimental effects were observed due to reductions in the strength of calcified protective plates and reductions in growth rates.

EMERGING PATTERNS OF VULNERABILITY: THE PHYSIOLOGICAL EVIDENCE

Some generalisations about the crustacean groups most likely to be affected by ocean acidification can be made by combining physiological responses from earlier studies on hypercapnia with those from recent experiments on long-term exposures to more moderate levels of pCO₂ (Pane & Barry 2007, Spicer et al. 2007, Widdicombe & Spicer 2008). To date, it appears that vulnerability to ocean acidification may be related to differences in lifestyle and to differences in the ability to compensate for environmental change. As stated previously, it is predicted that strong iono- and osmo-regulating species are likely to be the most tolerant to ocean acidification, simply because they have the compensatory mechanisms to respond to acid–base disruptions. These species tend to inhabit shallow coastal environments under freshwater influence, where they experience natural variations in seawater pCO₂, pO₂, salinity and temperature. For instance, when left behind in rock pools during the night, crabs can experience increased pCO₂ and decreased pH levels and pO₂ in the seawater (Truchot & Duhamel-Jouve 1980, Morris & Taylor 1983). Marine crustaceans can also be exposed to increased pCO₂ in deep-sea vent systems and in the surface waters of the open ocean where they also experience vertical gradients in pH and pO₂ (Fabry et al. 2008). Early physiological studies have demonstrated that the ability to compensate acid–base disturbances in the face of environmental change is highly variable among species. This is true among those species that have a subtidal distribution and experience stable conditions in their natural environment. For instance, aerial exposure and subsequent elevation of haemolymph CO₂ is fully compensated by the European lobster Homarus gammarus, is partially compensated by the edible crab Cancer pagurus and remains uncompensated in the swimming crab Necora puber and the spider crab Maja squinado (Taylor &
Whiteley 1989, Whiteley 1999). Moreover, physiological studies have shown that some species of intertidal crabs do not compensate for the effects of aerial exposure when exposed at low tide (Burnett & McMahon 1987). Instead they undergo metabolic depression and wait until the tide returns. Despite these differences in compensatory capacities, *N. puber* and *C. magister* are able to survive exposure to pCO₂ levels more relevant to ocean acidification, at least in the medium-term, i.e. up to 60 d (Pane & Barry 2007, Spicer et al. 2007, Small et al. 2010). Consequently, it remains unclear whether the ability of crustaceans to compensate for highly variable environments increases their tolerance to ocean acidification. However, this may have more to do with the limited data set collected to date and less to do with existing patterns of vulnerability. Clearly, there is a need to investigate the physiological responses in crustacean species from a broader range of marine habitats during exposure to relevant ocean acidification conditions for longer periods of time.

The ability to compensate for the effects of ocean acidification can also vary with lifestyle. Decapod crustaceans with high rates of activity have a greater capacity for passive compensation of haemolymph acid–base disturbances (i.e. buffering by non-bicarbonate buffers) than slow-moving, relatively inactive species due to species-related differences in respiratory variables. Relatively fast-moving species, such as the swimming crab *Necora puber*, have higher circulating levels of haemocyanin than slow-moving, relatively inactive crabs, such as *Maja squinado* (Watt et al. 1999). Higher haemocyanin levels lead to higher oxygen-carrying and non-bicarbonate-buffering capacities, in keeping with the higher aerobic requirements and higher rates of metabolic CO₂ production. The lower haemocyanin levels characteristic of slow-moving species are associated with relatively low rates of oxygen uptake and relatively high levels of circulating lactate levels, showing some reliance on anaerobic metabolism (Watt et al. 1999). Similar characteristics may contribute to the inability of the deep-sea tanner crab *Chionoecetes tanneri* to buffer an accumulating haemolymph acidosis when exposed to short-term hypercapnia (1% CO₂, ~1.28 kPa, for 24 h) (Pane & Barry 2007). For example, haemolymph protein levels were significantly lower in *C. tanneri* than those determined in a shallow-water species, *Cancer magister*, under the same conditions. The reduction in buffering capacity in *C. tanneri* was compounded by a failure to raise HCO₃⁻ levels beyond 3 mmol l⁻¹ (Pane & Barry 2007). The lack of compensatory ability could be explained by the low temperatures at which the measurements were taken (3°C) or by the fact that deep-sea crabs have low metabolic rates, in keeping with their habitation of a stable, harsh and resource-limited environment.

By inference, these observations suggest that other species living in similarly low-energy environments will be susceptible to ocean acidification. This is particularly pertinent at polar latitudes, where marine invertebrates are stenothermal, have poor thermal tolerances and are characterised by relatively low metabolic rates (Peck 2002, Pörtner et al. 2007). Acid–base characteristics have only been determined in 1 species of polar marine crustaceans, the giant Antarctic isopod *Glyptonotus antarcticus*. This species has relatively low circulating levels of protein, resulting in low haemocyanin oxygen-carrying and protein-buffering capacities (Whiteley et al. 1997). The latter is 2.5- to 7.5-fold lower than the range of values estimated in other aquatic crustaceans (Taylor & Taylor 1992). Not only is the lower buffering capacity a problem in terms of compensating for the effects of ocean acidification, the oxygen affinity of *G. antarcticus* haemocyanin is highly sensitive to a reduction in pH (Jokumsen et al. 1981). Both characteristics decrease the involvement of the respiratory pigment in the transport of oxygen from the gills to the tissues. It appears that *G. antarcticus*, just like the deep-sea crab *Chionoecetes tanneri*, will be unable to compensate for the effects of ocean acidification. As a result, both species will be more vulnerable to the associated changes in seawater chemistry.

**POTENTIAL ECOLOGICAL EFFECTS OF OCEAN ACIDIFICATION**

Very little information is available on the potential impacts of ocean acidification on the ecology of crustaceans. There is some evidence to show that ocean acidification may affect crustacean species at the population level by influencing the growth or reproductive performance of adults. In addition, there is a growing interest in the potential effects of ocean acidification on early life-cycle stages in benthic and pelagic crustacean species. Collectively, it appears that sensitivities to ocean acidification vary among species and with ontogeny. However, the lack of data makes it difficult to observe any emerging trends, and it is impossible to discuss the available information without resorting to individual studies.

**Effects of ocean acidification on growth rate**

The only evidence to date of the effects of elevated pCO₂/reduced pH on growth rates in adult crustaceans comes from 1 species of marine shrimp and 2 species of penaeid prawns (Wickins 1984, Kurihara et al. 2008). Growth rates in all 3 species were affected by elevated CO₂, but the marine shrimp *Palaemon pacificus* was
more sensitive than *Penaeus occidentalis* or *P. monodon* (Table 1). Not surprisingly, CO₂ had more of an effect when levels were increased and seawater pH was reduced to 7.6 pH units or lower. For example, when adult *P. pacificus* were held at a pCO₂ of 0.10 kPa (pH = 7.89 ± 0.05) there was no change in growth rate for 30 wk and then only in females (Kurihara et al. 2008). At the higher pCO₂ level of 0.20 kPa (pH = 7.64 ± 0.09), both growth rate and moult frequency decreased after 7 wk, and no animals survived beyond 15 wk. In penaeids, the growth rate declined when seawater pH fell below 7.4 due to a decrease in moultling frequency and an increase in intermoult period from 5 to 6–9 d (Wickins 1984).

**Effects of ocean acidification on reproduction and development**

Our understanding of the reproductive effects of ocean acidification in crustaceans is restricted to a small number of observations on egg production, and rates of embryonic and larval development (Table 1). Changes in egg production were observed in *Palaeomon pacificus* held at a pCO₂ of 0.10 kPa (Kurihara et al. 2008). Higher levels of pCO₂ (0.20 kPa), however, had no effect on egg production in the copepods *Acartia tunsisi* and *A. steueri* after 27 d of exposure (Kurihara et al. 2004a,b, Kurihara & Ishimatsu 2008) or in the barnacle *Amphibalanus amphitrite* held at pH 7.4 (McDonald et al. 2009). The influence of elevated CO₂ on embryonic development has only been investigated in 1 barnacle species, *Semibalanus balanoides*. In this intertidal species, a pCO₂ of 0.09 kPa reduced rates of embryonic development in isolated egg masses and delayed time to hatching by 19 d (Findlay et al. 2009).

In contrast, there is little evidence to show that ocean acidification is detrimental to larval and juvenile stages (Table 1). Currently, data on larval development under relevant levels of pCO₂ are available for 4 crustacean species: the copepod *Acartia tunsisi* (Kurihara & Ishimatsu 2008), the barnacle *Amphibalanus amphitrite* (McDonald et al. 2009), the lobster *Homarus gammarus* (Arnold et al. 2009) and the spider crab *Hyas*

Table 1. Effects of elevated seawater CO₂ on indices of growth and reproductive capacity in a variety of crustacean species. pCO₂: partial pressure of CO₂ calculated from values published as ppm (mole fraction) assuming a barometric pressure of 101.35 kPa. Dashes represent absence of available data

<table>
<thead>
<tr>
<th>Species</th>
<th>pCO₂ (kPa)</th>
<th>pH</th>
<th>Time</th>
<th>Effect</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acartia tunsisi</em></td>
<td>0.20</td>
<td>7.4</td>
<td>27 d</td>
<td>No effect on survival, body size, development rate, or egg production</td>
<td>Kurihara &amp; Ishimatsu (2008)</td>
</tr>
<tr>
<td><em>Calanus finmarchicus</em></td>
<td>0.8</td>
<td>6.85</td>
<td>72 h</td>
<td>No effect on adult growth, decrease in egg production</td>
<td>Mayor et al. (2007)</td>
</tr>
<tr>
<td><em>Acartia steueri</em></td>
<td>0.20–1.0</td>
<td>7.4–6.8</td>
<td>8 d</td>
<td>Decreased egg production at &lt;pH 6.8</td>
<td>Kurihara et al. (2004a,b)</td>
</tr>
<tr>
<td><em>Acartia erythraea</em></td>
<td>0.51–1.0</td>
<td>7.0–6.8</td>
<td>8 d</td>
<td>Decreased egg production at &lt;pH 6.8</td>
<td>Kurihara et al. (2004a,b)</td>
</tr>
<tr>
<td><em>Amphibalanus amphitrite</em></td>
<td>–</td>
<td>7.4</td>
<td>8–11 wk</td>
<td>No effect on growth or egg production</td>
<td>McDonald et al. (2009)</td>
</tr>
<tr>
<td><em>Semibalanus balanoides</em></td>
<td>0.09</td>
<td>7.7</td>
<td>104 d</td>
<td>Decreased survival</td>
<td>Findlay et al. (2009)</td>
</tr>
<tr>
<td><em>Penaeus occidentalis</em></td>
<td>–</td>
<td>7.6 &amp; 7.3</td>
<td>56 d</td>
<td>Decreased growth rates</td>
<td>Wickins (1984)</td>
</tr>
<tr>
<td><em>Penaeus monodon</em></td>
<td>–</td>
<td>7.9–6.4</td>
<td>36 d</td>
<td>Decreased growth rates</td>
<td>Wickins (1984)</td>
</tr>
<tr>
<td><em>Palaemon pacificus</em></td>
<td>1.0</td>
<td>7.9</td>
<td>30 wk</td>
<td>No effect on growth</td>
<td>Kurihara et al. (2008)</td>
</tr>
<tr>
<td></td>
<td>0.20</td>
<td>7.6</td>
<td>15 wk</td>
<td>Decreased growth and egg production</td>
<td>Kurihara et al. (2008)</td>
</tr>
<tr>
<td>Eggs/larvae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acartia erythraea</em></td>
<td>0.20–1.0</td>
<td>7.4–6.8</td>
<td>2d</td>
<td>Increase in nauplius mortality rates and hatching rate</td>
<td>Kurihara et al. (2004a,b)</td>
</tr>
<tr>
<td><em>Acartia tunsisi</em></td>
<td>0.20</td>
<td>7.4</td>
<td>27 d</td>
<td>No effect on development rate or hatching success</td>
<td>Kurihara &amp; Ishimatsu (2008)</td>
</tr>
<tr>
<td><em>Calanus finmarchicus</em></td>
<td>0.81</td>
<td>6.95</td>
<td>72 h</td>
<td>Decreased hatching success</td>
<td>Mayor et al. (2007)</td>
</tr>
<tr>
<td><em>Euphausia superba</em></td>
<td>1.0–2.0</td>
<td>7.7/7.4</td>
<td>26 d</td>
<td>Decreased hatching success</td>
<td>Kurihara &amp; Ishimatsu (2008)</td>
</tr>
<tr>
<td><em>Amphibalanus amphitrite</em></td>
<td>–</td>
<td>7.4</td>
<td>8–11 wk</td>
<td>No effect on larval condition, cyprid size and attachment, or metamorphosis</td>
<td>McDonald et al. (2009)</td>
</tr>
<tr>
<td><em>Semibalanus balanoides</em></td>
<td>0.09</td>
<td>7.7</td>
<td>104 d</td>
<td>Decreased rates of embryonic development, hatching and post-larval growth</td>
<td>Findlay et al. (2009, 2010b)</td>
</tr>
<tr>
<td><em>Echinogammarus marinus</em></td>
<td>0.20</td>
<td>7.5</td>
<td>18–20 d</td>
<td>No effect on rates of embryonic development or hatching number</td>
<td>Egilsdottir et al. (2009)</td>
</tr>
<tr>
<td><em>Gammarus locusta</em></td>
<td>0.10</td>
<td>7.6</td>
<td>–</td>
<td>No effect on growth rates to maturity</td>
<td>Haeum et al. (2009)</td>
</tr>
<tr>
<td><em>Palaemon pacificus</em></td>
<td>0.20</td>
<td>7.6</td>
<td>–</td>
<td>Decreased body size in settling juveniles</td>
<td>Kurihara et al. (2008)</td>
</tr>
<tr>
<td><em>Homarus gammarus</em></td>
<td>0.12</td>
<td>–</td>
<td>–</td>
<td>No effect on hatching number or rate of development</td>
<td>Arnold et al. (2009)</td>
</tr>
</tbody>
</table>
araneus (Walther et al. 2010). In all 4 species, elevation in pCO$_2$ to <0.02 kPa had no effect on rates of larval survival or development (Table 1). In addition, elevated pCO$_2$ had no effect on larval condition and cyprid size, attachment, or metamorphosis in A. amphitrite (McDonald et al. 2009). In H. gammarus, this may be due to the fact that the exoskeletons of planktonic decapod larvae (zoae) are unmineralised, while those of megalopae and benthic juveniles are only partially calcified (Anger 2001). This is likely to reduce the potential negative effects of ocean acidification on calcification rates during larval molts. Hatching success in the copepods Acartia erythraea and Calanus finmarchicus was negatively affected, but at pCO$_2$ levels of 0.50 to 0.80 kPa, which far exceed the values predicted for the year 2300 (Kurihara et al. 2004a,b, Mayor et al. 2007). In addition, the growth rates of early life stages of Semibalanus balanoides from the metamorphosing cyprids to early juveniles were significantly reduced by a decrease in seawater pH from 8.1 to 7.3 (~0.04 to 0.30 kPa) (Findlay et al. 2010b). A similar drop in pH (8.2 to 7.4), however, had no effect on juvenile to adult growth rates in the tropical barnacle A. amphitrite (McDonald et al. 2009). In addition, reductions in pH down to 7.8 (0.06 kPa) and 7.6 (0.10 kPa) had no effect on the growth rates of juveniles to adolescence or to sexual maturity in the amphipod Gammarus locusta (Hauton et al. 2009).

**COMBINED EFFECTS OF OCEAN ACIDIFICATION AND OTHER ENVIRONMENTAL VARIABLES**

Apart from some early work, the interactive effects of multiple stressors on the survival of marine crustaceans has been poorly studied, despite the fact that ocean acidification is occurring simultaneously with changes in temperature, salinity and oxygen. Early physiological studies on the effects of diurnal changes in temperature, pCO$_2$ and pO$_2$ that occur naturally in physiological studies on the effects of diurnal changes in temperature, salinity and oxygen. Early ocean acidification is occurring simultaneously with taceans has been poorly studied, despite the fact that of multiple stressors on the survival rates of larvae. In adult crustaceans, the physiological consequences of ocean acidification and temperature have been restricted to 2 species of subtidal crabs, Cancer pagurus and Hyas araneus (Metzger et al. 2007, Walther et al. 2009), and to a species of nektonic shallow-water prawn, Metapenaeus joyneri (Dissanayake & Ishimatsu 2011). In C. pagurus, exposure to 1% CO$_2$ (~1.0 kPa) and either a progressive decrease or increase in temperature reduced upper thermal limits and increased mortality rates (Metzger et al. 2007). A similar response was observed in the spider crab H. araneus, when exposed to more relevant pCO$_2$ levels of 0.07 and 0.30 kPa (Walther et al. 2009). An elevation in pCO$_2$ in H. araneus not only lowered the upper thermal tolerance limit, it also increased the heart rate and reduced haemolymph pO$_2$ levels when temperatures rose above 10°C. Collectively, these data suggest that thermal tolerances are reduced in crabs under high CO$_2$ conditions, due to a limitation in oxygen supply as described in teleost fishes by Pörtner & Farrell (2008). Elevated pCO$_2$ and temperature can also affect swimming performance, as exposure of M. joyneri to a pCO$_2$ of 1.0 kPa at 3 acclimation temperatures (10, 15 and 25°C) for 10 d significantly reduced critical swimming speeds (Dissanayake & Ishimatsu 2011). However, elevated pCO$_2$ had more of an effect on swimming performance than temperature, even though acclimation to the highest temperature (25°C) decreased aerobic scope (difference between standard and active metabolic rates). The authors attributed this observation to the fact that the prawns were held at temperatures outside their normal thermal optima (Dissanayake & Ishimatsu 2011). As a consequence, oxygen supply was restricted and aerobic performance was reduced. Given that reductions in
thermal tolerance windows have been linked to reductions in growth performance and reproductive activity, as well as reductions in biogeographical ranges and shifts in community composition, the combined effects of ocean acidification and temperature could have wide-ranging ecological implications (Pörtner 2002, 2010, Somero 2002, Pörtner & Farrell 2008).

Ecological studies have concentrated on the effects of elevated pCO2 and temperature on the growth and survival of post-larvae from 2 species of barnacles (Findlay et al. 2010a,b) and from the spider crab *Hyas araneus* (Walther et al. 2010). Even though both barnacle species were collected from similar intertidal habitats on the southwestern coast of England, differences in growth and shell development were observed between the cold-water species *Semibalanus balanoides* and the warm-water species *Elminius modestus* (Findlay et al. 2010a). Exposure to pCO2 levels of 0.04 and 0.10 kPa at 2 temperatures (14 and 18°C) had no effect on post-larval growth rates in *S. balanoides*, but the higher pCO2 and temperature treatment significantly reduced growth rates in *E. modestus*. In contrast, the shell calcium content in *S. balanoides* was reduced by CO2 and by temperature, but neither factor had any effect on the calcification rates in *E. modestus*. In summary, it appears that *S. balanoides* post-larvae are able to maintain growth, but at the expense of shell calcification. On the other hand, *E. modestus* post-larvae are able to maintain the integrity of their calcified shells, but at the expense of growth. The ability to maintain mineralised shell plates during elevated pCO2 and temperature exposure was attributed to differences in thermal tolerance brought about by sampling populations from different parts of their geographic distribution (Findlay et al. 2010a). Interestingly, a sub-arctic population of the cold-water species *S. balanoides* was observed to be more sensitive to CO2 than the population in southwestern England, at the southern limit of its distribution range (Findlay et al. 2010a,b). Growth and development of post-larval *S. balanoides* from Kongsfjorden, Svalbard, at 79°N, was negatively impacted by elevated CO2, but surprisingly an increase in temperature of +4°C had no effect (Findlay et al. 2010b). In contrast to the southern population, the northern population of *S. balanoides* also managed to maintain net calcification of their shells during elevated CO2, suggesting that resources were reallocated from 1 energy-demanding process to another as discussed in greater detail by Findlay et al. (2010b). Comparisons between populations of *H. araneus* from similar latitudes (temperate and sub-arctic) revealed that development time was slower in the northern compared with the southern population under present day pCO2 conditions (0.04 kPa) (Walther et al. 2010). An elevation in pCO2 to 0.30 kPa delayed rates of development and reduced growth rates and overall fitness of larvae from both populations. An increase in pCO2 to 0.07 kPa, however, had no effect. The megalopa emerged as the most vulnerable stage of development in *H. araneus*, as it was the most sensitive to temperature in the north and the most sensitive to CO2 levels in the south. The authors attributed the increase in sensitivity in the megalopa to reductions in thermal tolerance (Walther et al. 2010). They also predicted that both ocean acidification and global warming would affect the recruitment of the benthic juvenile stages in this species. A decrease in the abundance of *H. araneus* has already been observed in the North Sea around Helgoland, where temperatures have increased by 1.1°C over the last 40 yr (Walther et al. 2010).

Finally, the specific effects of elevated pCO2 and temperature on marine community diversity and structure have recently been addressed by using artificial substrate units planted on the shore at extreme low tide (Hale et al. 2011). After the establishment of marine invertebrate communities, the artificial substrate units were removed and exposed to 8 different treatments (4 pH levels at 2 different temperatures). After 60 d of exposure, the combination of low pH (7.3 and 6.7) and elevated temperature (16°C) significantly changed community structure and lowered diversity. However, at the higher pH levels (8.0 and 7.7) and elevated temperature, species abundance and diversity increased. Relevant to the present review was the fact that while molluscs and echinoderms were the most affected, and annelids the least, crustaceans showed an intermediate response. More specifically, gammaridean amphipods showed a marked decrease in abundance at low pH and elevated temperatures, but increased in abundance along with an isopod species at pH 7.7 and 7.3. Furthermore, the loss of the skeleton shrimp *Caprella acanthifera* from the higher temperature treatments contributed to changes in species richness. Overall this community-based mesocosm study revealed that the ecological impacts of the 2 environmental variables were greater than either factor in isolation. In addition, the study concluded that the changes in community structure were due to species-specific differences in tolerances (Hale et al. 2011). However, the authors stipulated that ecosystem-level responses to ocean acidification and global warming could not simply be explained by a reduction in individual performances. They also attributed the observed responses in species diversity to changes in community interactions, their argument being that the loss of the more vulnerable species provided opportunities for more tolerant species.

The dependence of community-led changes in marine ecosystems during ocean acidification on species-specific physiological tolerances has parallels to the
selective survivorship associated with the Permian-Triassic mass extinction, which occurred around 250 million yr ago (Pörtner et al. 2005, Knoll et al. 2007). This extinction event resulted in the loss of up to 54% of late Permian marine families, 68% of the genera and 92% of the species, resulting in a major re-organisation of the marine ecosystem. It has been argued that these ancient extinctions can be explained in terms of the physiological responses of marine invertebrates to the combined effects of environmental hypoxia, hypercapnia, sulphide toxicity and rising temperatures that prevailed at the time (Pörtner et al. 2005, Knoll et al. 2007). Moreover, the ability to compensate for hypercapnia is thought to be a key to survival. Interestingly, those groups that were more vulnerable to hypercapnia experienced significantly higher rates of extinction, although survival rates were also related to the presence or absence of a calcified exoskeleton and its relative proportion to soft tissues (Knoll et al. 2007). Arthropods were described by Knoll et al. (2007) as possessing a calcium carbonate skeleton of moderate mass with respect to supportive tissue and body fluids that were relatively well buffered. Although not the most vulnerable grouping, this group lost around 54% of its genera during the end-Permian mass extinction.

In summary, it appears that, in adult crustaceans, an increase in pCO2 to 1.0 kPa during an increase in temperature causes physiological disruption and has a synergistic effect on an individual’s performance. An increase in mortality rates was also observed in the subtidal crab Cancer pagurus (Metzger et al. 2007) and in the shallow-water prawn Metapenaeus joyneri during moulting (Dissanayake & Ishimatsu 2011). However, the sensitivity to multiple stressors varies among species, with differential effects on individual fitness and survival leading to changes in community structure and interactions in an intertidal marine community (Hale et al. 2011). Such differences could also explain selective survival during the end-Permian mass extinction when there was a diversity collapse in the marine environment (Knoll et al. 2007). Overall the combination of CO2 and temperature levels relevant to ocean acidification and global warming have little effect on the performance of post-larvae, at least in 2 species of barnacles (Findlay et al. 2010a,b). However, sensitivity does appear to change with life-cycle stage, as shown in Hyas araneus, where one particular stage of development was identified as being the most vulnerable (Walther et al. 2010). Moreover, sensitivity of early life stages to a single environmental variable can change within species according to geographical distribution (Findlay et al. 2010b, Walther et al. 2010). One population can be more sensitive to pCO2, while the other is more sensitive to temperature (Walther et al. 2010). Although investigations into the combined effects of elevated pCO2 and temperature in crustaceans are few and far between, there has only been 1 study on the effects of elevated pCO2 and reduced salinity. This is surprising given the role of ion and acid–base homeostasis in the determination of a species’ sensitivity to ocean acidification. In this particular study, the exposure of the intertidal amphipod Echinogammarus marinus to elevated CO2 (0.20 kPa) at 3 salinities (10, 22 and 35 psu) had little effect on hatching success and developmental rate (Egilsdottir et al. 2009). Overall, reductions in salinity were found to be more important than elevations in CO2.

CONCLUSIONS AND FUTURE DIRECTIONS

The main purpose of the present review was to summarise our current understanding of the potential biological effects of ocean acidification on marine crustaceans and to identify and characterise those species or groups most at risk. The study of marine crustaceans can make a valuable contribution to ocean acidification research because crustaceans occupy a wide variety of aquatic habitats and show a range of tolerances to environmental change. As a result they demonstrate a range of responses that can be used to increase our understanding of the mechanisms that determine tolerances to ocean acidification, as well as clarify the subsequent long-term effects on performance and survival. The physiological studies carried out to date suggest that the most vulnerable groups are those that are unable to compensate for the changes imposed by elevated pCO2 and reduced pH levels. These species tend to be poor iono- and osmoregulators, living in low-energy environments with low metabolic rates and low routine levels of activity, such as deep-sea and polar environments. From the limited data set, it appears that these species are characterised by low buffering capacities and a general inability to mobilise HCO3- ions from the seawater or from the exoskeleton to buffer the acid–base disturbances caused by ocean acidification. Moreover, they are highly specialised for living at low and stable temperatures and may be metabolically limited with respect to further change. Consequently the more vulnerable species are less likely to succeed in overcoming the combined effects of ocean acidification and increasing temperature or reduced salinity and PO2 levels resulting from climate change. In addition, they are less likely to be able to compete with warm-water invasive species that will be more adaptable and better able to exploit available resources. Crustacean species likely to be more tolerant of ocean acidification are those currently inhabiting fluctuating environments, such as estuaries and shallow coastal regions. These species are less likely to
suffer long-term reductions in fitness because they have the capacity to compensate acid–base disturbances via ion exchange mechanisms. The exceptions are slow-moving crabs with poor haemolymph-buffering capacities. The latter may be more vulnerable to ocean acidification due to their limited capacity to adjust their acid–base physiology. Overall, we still have little idea of how these various species will cope during prolonged exposure to elevated pCO₂ on a scale of months to years, or how multiple stressors will affect individual fitness. However, the indication is that concomitant changes in temperature, salinity and oxygen can have important synergistic effects.

Given the close association between physiological capacities and the ability to cope with ocean acidification, there is a continuing need to examine the mechanisms responsible for these compensatory responses. The relationship between ion regulation and acid–base balance is still far from clear. Even less is known about the mechanisms underlying calcification processes in crustaceans. All 3 physiological processes, i.e. iono-regulation, acid–base balance and calcification, could be linked via the mobilisation of Ca²⁺ and HCO₃⁻ from the exoskeleton (Whiteley 1999). In addition, it is unclear whether those species that can tolerate ocean acidification will be able to maintain compensatory responses over time, and whether less tolerant species will be able to acclimatise or even adapt to the changes in seawater carbonate chemistry. Future studies are needed to examine physiological and ecological responses to ocean acidification in crustacean species with differing tolerances to environmental change over longer time intervals at relevant pCO₂ levels and in combination with changes in temperature, salinity, or oxygen levels. The resulting data can then be used to inform on the groups of crustaceans most likely to be adversely affected by ocean acidification and climate change. It can also be used to explain patterns of vulnerability in other marine taxa. In addition, it is vital that we increase our understanding of the capacity of marine crustaceans to adapt to the effects of ocean acidification. Such information will help towards forecasting the potential long-term effects of ocean acidification and climate change on marine ecosystems (Kurihara 2008). Even though a few multi-generation experiments have been conducted to date (Kurihara & Ishimatsu 2008), many more are needed in order to examine the potential for adaption under future ocean acidification scenarios.

Currently, there is little evidence to suggest that early life stages are more vulnerable to ocean acidification than adults, but the data set is extremely limited. Recent work suggests that survival rates are affected and subtle changes in the ability to calcify the exoskeleton during growth by moulting may have long-term repercussions for survival and recruitment. From the 2 barnacle species studied to date, it appears that ocean acidification and climate change will not affect post-larval survival (Findlay et al. 2010a,b), but sensitivities can vary with stage of development (Walther et al. 2010). In addition, it has been shown that ocean acidification can affect growth rates and moulting frequencies in crustaceans (Kurihara et al. 2008, Dissanayake & Ishimatsu 2011). Further work is needed to determine whether this is a general effect or whether it is species specific. If moulting frequencies and mortality rates in crustaceans are more generally affected by ocean acidification, this could have a profound effect on species survival, distribution and abundance. Overall, future studies are needed to identify any potential bottlenecks during development and to examine the combined effects of ocean acidification and other environmental variables on the survival of early life stages from crustacean species with differing tolerances to environmental change. Although marine crustaceans are currently considered to be broadly tolerant of ocean acidification, closer examination reveals that certain species and developmental stages could be adversely affected. It is important that the scientific community considers the impacts of ocean acidification and climate change on representatives from all marine invertebrate phyla in order to truly appreciate the resulting effects on species richness, community structure and function, and ecosystem processes.

Acknowledgements. This review was prepared as part of 2 research projects: Impacts of ocean acidification on key benthic ecosystems, UK Ocean Acidification Research Programme funded by DEFRA, NERC and DECC; and SUSFISH, a project funded by the European Regional Development Fund through the Ireland Wales Programme (INTERREG 4A).

LITERATURE CITED


Findlay HS, Kendall MA, Spicer JI, Widdicombe S (2010b) Relative influence of ocean acidification and temperature on intertidal post-larvae at the northern edge of their geographic distribution. Estuar Coast Shelf Sci 86:675–682


→ Santos LCF, Belli NM, Augusto A, Masui DC, Leon FA, McNamara JC, Furriel RPM (2007) Gill (Na⁺, K⁺)-ATPase

*Submitted: November 29, 2010; Accepted: April 28, 2011*

*Proofs received from author(s): May 13, 2011*