

Predicting the Effects of Ocean Acidification on Predator-Prey Interactions: A Conceptual Framework Based on Coastal Molluscs

KRISTY J. KROEKER^{1,*}, ERIC SANFORD^{1,2}, BRITTANY M. JELLISON^{1,2}, AND BRIAN GAYLORD^{1,2}

¹*Bodega Marine Laboratory, University of California Davis, Bodega Bay, California 94923; and*

²*Department of Evolution & Ecology, University of California Davis, One Shields Ave, Davis, California 95616*

Abstract. The influence of environmental change on species interactions will affect population dynamics and community structure in the future, but our current understanding of the outcomes of species interactions in a high-CO₂ world is limited. Here, we draw upon emerging experimental research examining the effects of ocean acidification on coastal molluscs to provide hypotheses of the potential impacts of high-CO₂ on predator-prey interactions. Coastal molluscs, such as oysters, mussels, and snails, allocate energy among defenses, growth, and reproduction. Ocean acidification increases the energetic costs of physiological processes such as acid-base regulation and calcification. Impacted molluscs can display complex and divergent patterns of energy allocation to defenses and growth that may influence predator-prey interactions; these include changes in shell properties, body size, tissue mass, immune function, or reproductive output. Ocean acidification has also been shown to induce complex changes in chemoreception, behavior, and inducible defenses, including altered cue detection and predator avoidance behaviors. Each of these responses may ultimately alter the susceptibility of coastal molluscs to predation through effects on predator handling time, satiation, and search time. While many of these effects may manifest as increases in *per capita* predation rates on coastal molluscs, the ultimate outcome of predator-prey interactions will also depend on how ocean acidification affects the specified predators, which also ex-

hibit complex responses to ocean acidification. Changes in predator-prey interactions could have profound and unexplored consequences for the population dynamics of coastal molluscs in a high-CO₂ ocean.

Introduction

Although environmental change fundamentally affects individuals, all organisms are embedded in complex networks of species whose interactions regulate populations and structure communities. The emergent effects of environmental change on any one species will therefore depend on its interactions with others (Sanford, 1999; Harley, 2011; Kroeker *et al.*, 2013b). Despite this knowledge, our understanding of the effects of environmental change on the outcomes of species interactions is very limited (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010; Zarnetske *et al.*, 2012). Among possible interactions, predation often plays a central role in structuring natural communities (Estes and Palmisano, 1974; Paine, 1974; Carpenter *et al.*, 1986), and the effects of environmental change on predator-prey interactions could disproportionately influence community structure in the future (Sanford, 1999; Zarnetske *et al.*, 2012).

Ocean acidification (OA), which is characterized by a shift in seawater carbonate chemistry due to the oceanic uptake of atmospheric carbon dioxide (CO₂) and results in decreased seawater pH and carbonate ion concentration, is one of the most pervasive environmental changes in the ocean (Feely *et al.*, 2009). There has been an enormous scientific effort to understand the physiological effects of these ongoing changes in ocean chemistry, and laboratory-based research suggests that OA can reduce the net calcification, growth, reproduction, and survival of a wide range

Received 26 November 2013; accepted 17 April 2014.

* To whom correspondence should be addressed. E-mail: kjkroeker@ucdavis.edu

Abbreviations: OA, ocean acidification.

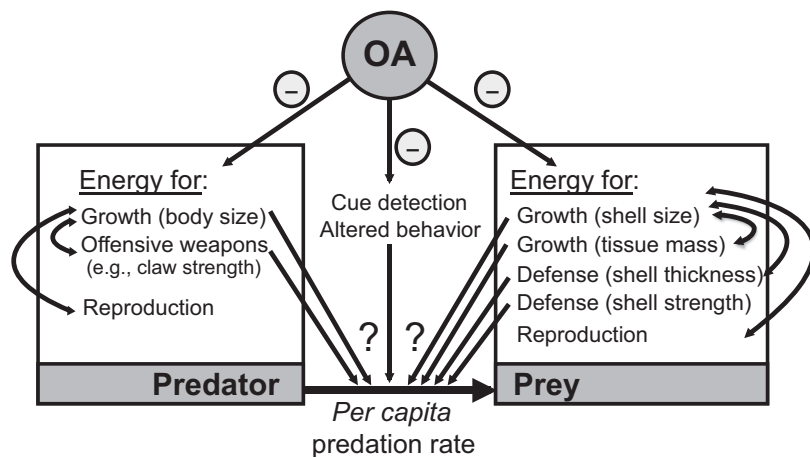


Figure 1. Conceptual model of the pathways through which ocean acidification may affect *per capita* predation rates in coastal molluscs. Arrows within boxes symbolize the potential for trade-offs among defenses/offenses, growth, and reproduction.

of marine species (Kroeker *et al.*, 2010, 2013a). Despite a growing understanding of species' vulnerabilities, however, it remains unclear how the direct effects of OA on individual species might scale up to impact population dynamics and communities. Experiments examining the indirect effects of OA on individual species *via* altered species interactions are still rare, and the few multi-species studies available suggest that large-scale community shifts associated with OA are mediated in part by interactions among species (Wootton *et al.*, 2008; Connell *et al.*, 2013; Kroeker *et al.*, 2013b). The initial research on the subject has primarily focused on the importance of altered competition for space in high-CO₂ conditions, but the degree to which perturbed predator-prey dynamics influence community shifts remains unknown.

Although OA affects a broad range of marine species, those that build a shell or skeleton out of calcium carbonate appear especially vulnerable (Kroeker *et al.*, 2013a). OA increases the energy required to produce and maintain calcified structures (Cohen and Holcomb, 2009; Melzner *et al.*, 2011; Waldbusser *et al.*, 2013) and can reduce net calcification (Orr *et al.*, 2005; Gazeau *et al.*, 2007; Talmage and Gobler, 2010). Many marine species rely on these calcium carbonate shells as defense from predators (Vermeij, 1993), and reductions in net calcification could increase species' susceptibility to predation. The consequences of OA on predator-prey interactions are, however, likely to extend beyond its impacts on net calcification. Calcification is but one of many important physiological processes, and the total energy available to calcified species must be allocated among defenses (including calcification, inducible defenses, avoidance behaviors, and immune responses), growth, and reproduction. Because trade-offs exist among these processes (Palmer, 1981; Trussell and Nicklin, 2002), energy

allocation among them could influence *per capita* predation rates (Fig. 1).

There is increasing evidence that some species may be capable of maintaining calcified structures under conditions of OA, but that this maintenance requires more energy (Palmer, 1981, 1992). When food or energy is abundant, some species may be able to simply acquire the additional energy necessary to maintain calcification by increasing feeding rates (Melzner *et al.*, 2011; Thomsen *et al.*, 2013), with little-to-no trade-off in growth or reproduction. However, when food is not plentiful or energy is otherwise limited, calcified species may confront two outcomes: (1) calcified structures may become thinner or weaker (Talmage and Gobler, 2010; Gaylord *et al.*, 2011; Amaral *et al.*, 2012) or (2) net calcification may be maintained at the expense of growth, reproduction, or other defenses (Wood *et al.*, 2008; Stumpp *et al.*, 2011; Waldbusser *et al.*, 2013). Energy reallocation to calcification may then result in reduced body size, energetic content, inducible defenses, or immune responses of calcified species in acidified conditions (Fig. 2). Moreover, emerging evidence suggests that OA may have complex neurological effects that impair chemoreception, learning, and other behaviors important for predator avoidance (Munday *et al.*, 2009; Nilsson *et al.*, 2012; Watson *et al.*, 2013). While many of these changes could increase *per capita* predation rates on calcified prey, the emergent effects are further complicated by potential effects of OA on the predator (Fig. 3).

Decreased thickness or strength of shells, reduced body size, lower energetic content, reduced immune responses, attenuated inducible defenses, or impaired chemoreception and behavior could each increase the susceptibility of calcified marine species to predation, depending on the ability of predators to take advantage of these effects (Fig. 1).

Species		Shell thickness or strength	Shell size	Energetic content	Adaptive Behavior	Predation pressure	Reference
<i>Ostrea lurida</i>		=	↓			↑	Sanford <i>et al.</i> (2014)
<i>Mercenaria mercenaria</i>		↓	↑	↑			Dickinson <i>et al.</i> (2013)
<i>Mytilus edulis</i>		=	=	=			Hiebenthal <i>et al.</i> (2013)
<i>Arctica islandica</i>		=	=	=			
<i>Concholepas concholepas</i>		=			↑		Manriquez <i>et al.</i> (2013)
<i>Littorina littorea</i>		↓	=				Metalunan <i>et al.</i> (2013)
<i>Saccostrea glomerata</i>		↓				↑	Amaral <i>et al.</i> (2012)
<i>Bembicium auratum</i>		↓	=				
<i>Mytilus californianus</i> *		↓	↓	↓			Gaylord <i>et al.</i> (2011)
<i>Crassostrea virginica</i>		↓		↓			Beniash <i>et al.</i> (2010)
<i>Argopecten irradians</i> *			=	=			Talmage and Gobler (2010)
<i>Crassostrea virginica</i> *			↓	=			
<i>Mercenaria mercenaria</i> *			=	=			
<i>Littorina littorea</i>		↓				↑	Bibby <i>et al.</i> (2007)

Figure 2. Examples of studies that have measured more than one of the traits identified as important in predator-prey dynamics. An equal sign (=) denotes no significant change, a downward-facing arrow denotes a reduction in the given parameter, and an upward-facing arrow denotes an increase in that parameter. An asterisk (*) denotes an experiment on larvae. When the experiment manipulated more than one factor (e.g., temperature or salinity), the effect of ocean acidification is reported only at the ambient level of the second factor.

However, the interactions between predators and calcified prey exposed to OA have rarely been experimentally tested. Here, we discuss the potential effects of OA on predator-prey interactions involving coastal molluscs. We focus on coastal molluscs because some, such as oysters and mussels, are key foundation species in both coastal and estuarine environments (Suchanek, 1992; Beck *et al.*, 2011), rely on calcified shells as defense from predators, and have been shown to be especially vulnerable to OA (Michaelidis *et al.*, 2005; Gazeau *et al.*, 2007; Talmage and Gobler, 2010; Gaylord *et al.*, 2011; Barton *et al.*, 2012). Moreover, oyster and mussel beds provide habitat for a wide range of species, support local economies through fisheries and aquaculture, maintain water quality through filtering, and provide numerous other ecosystem services. Here, we build upon ecological theory and the nascent experimental evidence of OA's effects on species interactions and trade-offs among traits in coastal molluscs (Fig. 2) to develop a conceptual framework for the effects of OA on predator-prey dynamics more broadly (Fig. 3).

Effects on defenses

Although shells protect molluscs from physical stresses, including heat, desiccation, and wave forces (Garrity, 1984), they function primarily as a defense against predators. Co-evolution between predatory crabs and their gastropod prey has led to increased shell thickness and sculpturing in marine gastropods and bivalves for defense (Vermeij, 1982, 1993). Moreover, some molluscs exposed to cues from their predators increase shell thickness as an inducible defense (Appleton and Palmer, 1988; Trussell, 1996). While many mollusc species also use habitat or density refugia to avoid encounters with predators (Menge and Lubchenco, 1981), sessile species that cannot move to escape predators, such as oysters and mussels, rely for defense primarily on shell thickness or muscular resistance to having their valves penetrated or forcibly opened.

Calcified prey allocate a large amount of energy to shell growth as a defense against predators (Palmer, 1992). As OA causes calcification to become more costly, it may result in thinner or weaker shells for some species (Talmage and Gobler, 2010; Thomsen *et al.*, 2010; Metalunan *et al.*, 2013). Reduced shell thickness or strength could decrease the effort or amount of time necessary for boring or drilling predators to penetrate mollusc shells. For example, in a study of the shell growth and predation susceptibility of the rock oyster *Saccostrea glomerata*, individuals of the same size were collected from estuaries that are naturally more acidic (pH values below 7.6 were caused by caustic sulfate soil runoff) as well as from control estuaries; the oysters were then exposed to predatory snails. The snails spent 20% less time handling the oysters from the more acidic sites, which was attributed to relatively minor reductions in shell

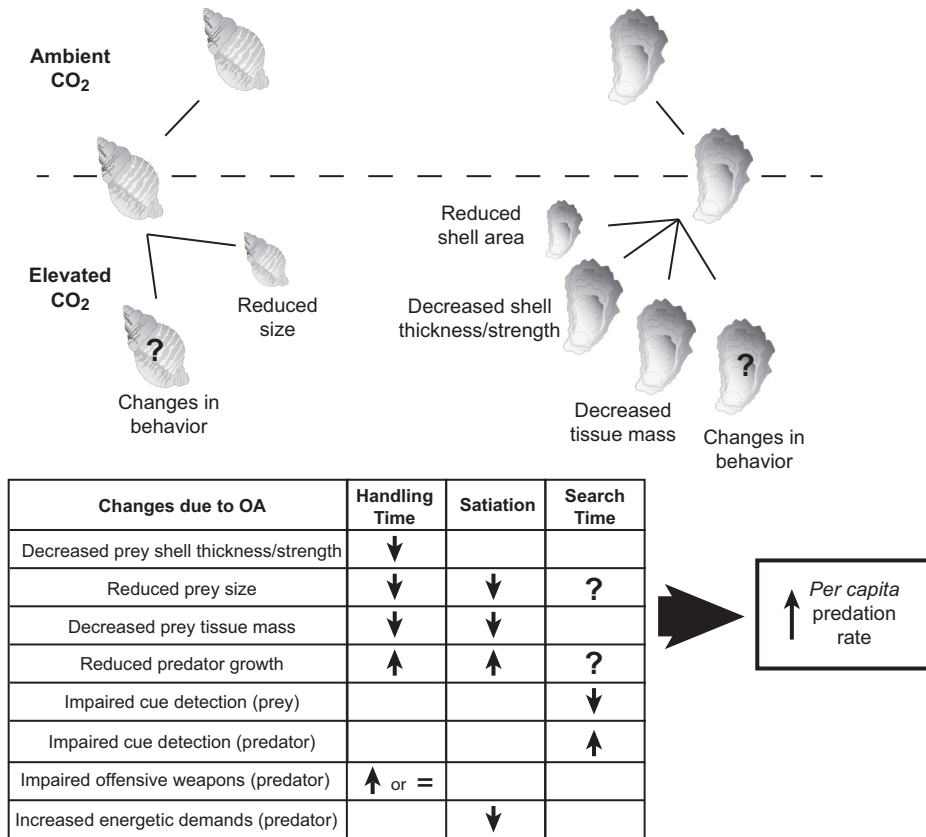


Figure 3. Implications of energetic trade-offs and behavioral effects on factors influencing predator-prey dynamics: handling time, satiation, and search time.

strength (Amaral *et al.*, 2012). Furthermore, a reduction in shell thickness can also reduce the force necessary to break the shell (McDonald *et al.*, 2009; Beniash *et al.*, 2010; Gaylord *et al.*, 2011; Amaral *et al.*, 2012), suggesting that molluscs could also become more susceptible to crushing predators such as crabs in acidified conditions, depending on the ability of predators to crush shells in high-CO₂ conditions (Landes and Zimmer, 2012). An enhanced susceptibility to increased predation due to thinner or weaker shells may be especially pronounced among sessile, calcified prey that rely heavily on shells for defense (Amaral *et al.*, 2012).

Energy allocation strategies that result in thinner or weaker shells in high-CO₂ conditions may still prove successful in some environments with low predation pressure. Although the conditions at deep-sea volcanoes are imperfect analogs for CO₂-driven ocean acidification, these systems can still illustrate the importance of predation on the demographics of molluscs in acidified conditions. Tunnicliffe *et al.* (2009) found abundant populations of the deep-sea mussel *Bathymodiolus brevior* in the highly acidic conditions caused by liquid CO₂ and hydrogen sulfide emissions surrounding a submarine volcano (mean pH values ranging from 5.4 to 7.3). While shells were substantially thinner in

the acidic conditions compared to those of mussels collected from other deep-sea sites, the mussels were still able to survive (Tunnicliffe *et al.*, 2009). The mussels' shells dissolved rapidly if the protein layer covering the outside of the shells (*i.e.*, the periostracum) was even slightly damaged, and the ability of these organisms to cope with low pH was attributed to the absence of predators that might otherwise have consumed the mussels or disturbed the shells' resistant covering. This trend suggests that the mussels could physiologically survive in the very acidic environment with thinner, weaker shells, but that their persistence in this state could in large part depend on the absence of predation pressure.

Elevated CO₂ has also been shown to disrupt other defenses in molluscs, such as attachment strength in sessile species (O'Donnell *et al.*, 2013) or inducible defenses such as shell thickening in response to predator cues (Bibby *et al.*, 2007). In a study examining inducible defenses of littorine snails, the snails exposed to cues from their crab predators in ambient seawater produced 30% thicker shells (Bibby *et al.* 2007). However, snails raised in highly elevated CO₂ concentrations (~14,000 μatm pCO₂) showed no sign of shell thickening when exposed to a predator cue.

Instead, the snails raised in acidified conditions with predator cues crawled out of the water to avoid contact with the predator, effectively using behavioral responses in place of the morphological, inducible defenses (Rundle *et al.*, 2004). Predator avoidance behaviors could, however, have indirect effects on the growth and population dynamics of coastal molluscs due to non-consumptive effects (*e.g.*, reduced time available for foraging [Peacor and Werner, 2001]), which are discussed in more detail in a following section. In addition, some bivalve species increase their byssal thread production and attachment strength in response to predators that pull them from the substrate (Leonard *et al.*, 1999). OA has been shown to weaken the byssus of mytilid mussels, which could increase susceptibility to predation. In addition, byssus secretion has an energetic cost (Babarro *et al.*, 2008), and OA could hypothetically cause a trade-off between calcification, growth, reproduction, and byssus secretion that would also affect predator-prey interactions.

Effects of reduced prey size on predation risk

In contrast to those species that experience reduced net calcification and defense when exposed to elevated CO₂, some prey species may be able to maintain shell thickness, strength, and defense at the expense of growth and body size. A reduction in the size of calcified prey can affect predator-prey dynamics *via* size-dependent predation. Large body size can reduce susceptibility to predation because predators may be less able to handle larger prey (Thompson, 1975; Vermeij, 1993). In addition, larger bivalves typically have stronger adductor muscles that allow them to more powerfully hold their shell closed when under attack from predators that pry shells open (*e.g.*, seastars, some crustaceans and gastropods) (Kautsky *et al.*, 1990; Norberg and Tedengren, 1995). Thus, smaller individuals are often at higher risk of predation, and trade-offs resulting in slower growth or reduced overall size could also increase predation risk regardless of the shell properties of the prey.

A reduction in size is a common response in molluscs exposed to OA (Talmage and Gobler, 2010; Crim *et al.*, 2011; Gaylord *et al.*, 2011; Hettlinger *et al.*, 2012; Kroeker *et al.*, 2013a; Waldbusser *et al.*, 2013), and smaller body size could also lead to decreased handling times and higher *per capita* predation rates on many calcified prey, depending on the predator. For example, in an experiment with the Olympia oyster *Ostrea lurida*, invasive predatory snails consumed 20% more oysters from high-CO₂ concentrations than from control conditions (Sanford *et al.*, 2014). Although shell thickness did not differ among oysters of the same size in control and high-CO₂ conditions, the oysters were significantly smaller, suggesting a reallocation of energy to maintain calcification in the acidified conditions. Thus, increased predation was attributed to predatory snails consuming the smaller individual prey items more quickly

in acidified conditions. Because smaller individuals naturally have thinner shells than bigger individuals, the smaller size of oysters raised in elevated CO₂ did effectively result in thinner shells, which could also have contributed to the decreased handling time by predators (Sanford *et al.*, 2014).

Effects on prey energetic content and quality

While a reduction in the size of molluscan prey exposed to OA could increase *per capita* predation rates *via* reduced handling times or by enabling predators to feed on prey items they could not consume before, it could also increase predation pressure through a concurrent decrease in the energetic content per individual (Wood *et al.*, 2008). For example, in an experiment examining the effects of near-future OA on larval mussels of the species *Mytilus californianus*, high CO₂ (~1000 μ atm CO₂) resulted in a 33% mean reduction in dry tissue mass per individual (Gaylord *et al.*, 2011). Predators would thus receive substantially less energy per mussel consumed and would need to consume more individuals to maintain their energetic needs. Likewise, the total lipid content of larval bivalves has been found to decrease with OA (Talmage and Gobler, 2011).

A reduction in tissue mass or energetic content can influence predation rates even when the shell size is maintained. For example, predatory gastropods given the choice of rock oysters of similar sizes collected from naturally more acidic estuaries and control estuaries showed no preference for either type of oyster in their initial attack, but less than half of the snails that consumed a non-acidified control oyster as a first or second prey choice continued to consume additional oysters (~41%) (Amaral *et al.*, 2012). In contrast, almost all of the snails that consumed two acidified oysters as their first and second choices went on to consume more oysters (~83%) (Amaral *et al.*, 2012). While other factors, such as decreased handling time due to minor decreases in shell strength, were not ruled out, these results suggest that the prey from acidified conditions with shell sizes similar to those from non-acidified control conditions did not satiate predators when compared to oysters from control conditions. It is yet unclear whether this effect might be due to decreases in energetic content (*i.e.*, reduced tissue mass) or even decreases in energetic quality (*e.g.*, reduced calories per tissue mass) as has been shown in non-molluscan taxa (Rossoll *et al.*, 2012).

Altered host-parasite interactions

Parasite-host interactions are a specialized form of predator-prey interactions that might also be influenced by OA through energetic trade-offs. Coastal molluscs are host to a variety of parasites, from trematode flatworms to nematodes and gregarine protozoans (Kim and Powell, 2007). As in other invertebrates, molluscs use immune responses as primary defense against their parasites, including the common

parasitic larval stages of trematodes (Bayne *et al.*, 2001). Although the effects of OA on host-parasite interactions of molluscs have not been experimentally tested, several studies have reported a modulation of immune responses among different invertebrates in high CO₂ (Bibby *et al.*, 2008; Hernroth *et al.*, 2011; Dupont and Thorndyke, 2012; Matozzo *et al.*, 2012), suggesting that OA could influence the interaction between parasites and coastal molluscs.

Invertebrates rely primarily on innate immunology to defend themselves against parasites and pathogens (Rolff and Siva-Jothy, 2003). As with shell defenses, immune responses are thought to have physiological costs whose energy could otherwise be dedicated to growth or reproduction (Sheldon and Verhulst, 1996; Moret and Schmid-Hempel, 2000; Rolff and Siva-Jothy, 2003). Trade-offs in fitness parameters due to an immune response are generally expected when the immune response is especially robust or when resources are limiting (Moret and Schmid-Hempel, 2000; Sandland and Minchella, 2003). Given that OA could increase the physiological costs of maintenance *via* acid-base regulation and calcification, the energy available for immune responses may be reduced with OA when resources are limiting.

Among molluscs, phagocytosis is a common defense against small parasites, including the sporocytic stage of trematodes (Bayne *et al.*, 2001). An initial study of immune responses in the blue mussel *Mytilus edulis* (Bibby *et al.*, 2008) found a reduction in phagocytic activity in high CO₂, suggesting a suppression of the immune system with OA. While the change in the immune response could have been caused by an energetic trade-off in high CO₂ in which calcification, growth, or maintenance was prioritized, the mechanisms for this response were not explicitly tested. The altered immune response could also have been caused by changes in the internal concentrations of key ions that are used for cell signaling in immune responses (Bibby *et al.*, 2008). Several studies have reported a complex modulation of other immune responses of several invertebrate species in high-CO₂ conditions (Bibby *et al.*, 2008; Hernroth *et al.*, 2011; Dupont and Thorndyke, 2012; Matozzo *et al.*, 2012; Asplund *et al.*, 2013), and more experiments are needed to understand whether the susceptibility of molluscs to parasites will change in high CO₂.

Altered behavioral responses of prey

Mobile molluscs may also compensate for reduced defenses under conditions of OA by changing their behaviors, such as avoiding predators by moving locations or hiding within protected environments (Bibby *et al.*, 2007). However, modifying behavior to reduce predation risk can still negatively affect prey species because they spend less time foraging or more time fleeing, thereby causing a reduction in growth or reproductive output (*i.e.*, non-consumptive

effects [Pressier *et al.*, 2005; Railsback and Harvey, 2013]). This points to another possible form of trade-offs among defense (in this case adaptive behavior), growth, or reproduction.

Adaptive behaviors require that organisms be able to sense their environment and perceive predation risk; however, there is mounting evidence that OA can also cause dramatic neurological changes that affect a species' ability to detect cues and alter its behavior. While data for molluscs are sparse, initial studies of juvenile reef fish demonstrate surprising maladaptive attraction to the odors of unsuitable habitat and predators under elevated CO₂ (Dixon *et al.*, 2010; Munday *et al.*, 2010; Ferrari *et al.*, 2011). This olfactory impairment results in riskier behavior and higher mortality when fish reared in high CO₂ are released into the wild with predators (Munday *et al.*, 2010). Additionally, fish reared under elevated CO₂ also show altered auditory preferences (Simpson *et al.*, 2011), loss of predator avoidance behaviors (Domenici *et al.*, 2012), and a disruption of associative learning (Ferrari *et al.*, 2012). Recent evidence suggests that the behavioral changes could be linked to a more systemic change in neurotransmitter function, specifically the GABA-A receptor common to vertebrate brains (Nilsson *et al.*, 2012; Chivers *et al.*, 2013).

Although most research concerning behavioral effects of OA has focused on fish, emerging evidence suggests there may be complex effects on invertebrate behavior as well (de la Haye *et al.*, 2011, 2012; Manríquez *et al.*, 2013; Watson *et al.*, 2013). Recent research on molluscs suggests that some of the effects of OA on invertebrate behavior may also be a result of specific neurological changes. GABA-like receptors are also found in many invertebrates, including molluscs (Hutton *et al.*, 1993; Stewart *et al.*, 2011). Watson *et al.* (2013) found that the predator avoidance behaviors (*i.e.*, the choice to jump away from a predator, the speed at which they jumped, as well as the distance they moved after jumping) of the marine gastropod *Gibberulus gibberulus gibbosus* were significantly reduced by exposure to elevated CO₂. When exposed to cues from a predator, the percentage of snails that jumped was almost halved in high-CO₂ conditions, while it took the high-CO₂ snails that did jump almost twice the time to do so (Watson *et al.*, 2013). As in the previous studies with fish, differences in behavior due to metabolic changes or the deterioration of the chemical cue in high CO₂ were ruled out. For example, the snails were able to right themselves at similar rates in both control and elevated CO₂ conditions, suggesting that locomotion itself was not impaired. Instead, treatment with the GABA-A inhibitor (gabazine) restored the predator avoidance behaviors, suggesting that the altered behavioral responses in high CO₂ were due to neurological dysfunction. An altered ability to detect or avoid predators due to OA could also increase the *per capita* predation rate of molluscs by reducing the search times necessary for predators to locate prey.

Effects on predators

The emergent effects of OA on predator-prey dynamics depend on predators' responses to OA. OA is likely to be energetically costly for all species as they work to maintain their acid-base balance in lower pH conditions (Ishimatsu *et al.*, 2008). A general increase in the metabolic costs of all species, including predators, could reduce predator populations through basic energetic constraints (*i.e.*, there is less energy available to move through a food web). In addition, increased metabolic costs could also result in slower growth or reduced body sizes among predators whether they were calcified or not. Many predator-prey interactions are size-structured (Paine, 1976), and a reduction in predator size could reduce the preferred prey size as well (Hughes and Dunkin, 1984). In addition, reduced predator size could reduce the size of prey that a predator is able to successfully capture and consume (Dayton, 1971; Paine, 1976), or increase its handling time of prey.

Due to their carbonate shells, calcified predators, such as gastropods or crustaceans, may be most likely to suffer reductions in net calcification or growth in more acidic conditions. Among these calcified predators, feeding modes may provide insight into which types of predators may be more vulnerable to OA. For example, the success of predatory gastropods that use their chitinous radulas and acidic secretions to bore a hole in shells of prey may be less affected by OA because it is independent of their own shell thickness or strength (Amaral *et al.*, 2012; Sanford *et al.*, 2014). In contrast, predators that rely on muscle strength to crush or pry open shells might be more susceptible to OA. For example, energy reallocation in calcified species has been shown to reduce muscle mass in sea stars (Wood *et al.*, 2008), and evidence suggests that OA could reduce the claw strength in predatory crabs (Landes and Zimmer, 2012). In contrast, most research suggests that OA does not significantly affect the growth of fishes (Kroeker *et al.*, 2013a); thus the size of fish predators may be maintained in high-CO₂ conditions, allowing them to take advantage of more poorly defended prey. Last, there is limited evidence regarding how OA may affect the growth of parasites. Previous research has shown that parasites with free-living stages are susceptible to other environmental stressors, including pH in freshwater habitats (Lafferty, 1997), suggesting that parasites may be sensitive to changes in pH caused by OA as well.

Increased energetic demands of predators due to the physiological effects of OA could also increase predation rates in some species (Gooding *et al.*, 2009). Regulation of internal acid-base balance in elevated CO₂ conditions may require more energy for maintenance among all predator types (Ishimatsu *et al.*, 2008). As with molluscan prey, this energy could either be reallocated from growth or reproduction or gained through an increase in feeding rate if prey are

available and if consumption rates can be increased (*e.g.*, type I vs. type II functional responses to prey density). This may serve to increase the predation rates across a range of consumer types. In contrast, OA could also result in metabolic depression in those predators that are unable to regulate intracellular pH, which could lead to decreased feeding rates among some species (Rosa and Seibel, 2008; Appelhans *et al.*, 2012). Generally, highly active, mobile species are more capable of regulating their acid-base balance (*e.g.*, fishes, brachyuran crustaceans, but see Rosa and Seibel, 2008) than more sedentary species (Pörtner, 2008; Melzner *et al.*, 2009).

It is yet unclear whether marine predators actually prefer prey species from acidified conditions or are able to detect a difference between prey from acidified and non-acidified environments. A few choice experiments with prey raised in acidified and non-acidified conditions have been conducted (Amaral *et al.*, 2012; Landes and Zimmer, 2012; Sanford *et al.*, 2014), but with differing results. For example, predatory crabs given the choice of littorine snails raised in elevated CO₂ or control conditions did not show a preference for high-CO₂ prey despite potential differences in shell strength and handling time (Landes and Zimmer, 2012). In fact, the crabs always preferred larger snails (regardless of treatment) even if the outcome was predictably less successful (Landes and Zimmer, 2012). This pattern may represent a specific strategy for this species of crab to obtain the relatively high energetic content in large snails regardless of the potential increase in handling time (*i.e.*, optimal foraging strategy). Similarly, predatory snails given the choice of oysters from estuaries acidified from sulfate soils and control estuaries showed no preference in their initial attacks (Amaral *et al.*, 2012). However, in a different choice experiment with a predatory snail (*Urosalpinx cinerea*) that was offered native *Olympia* oysters from high- and low-CO₂ treatments together, the snails tended to consume more high-CO₂ oysters than would be expected on the basis of predation rates when the two types were offered separately (Sanford *et al.*, 2014). There is evidence that this species of snail could detect differences in metabolic rates of oysters through cues in the excreted waste (Blake, 1960), but this possibility has not been explicitly tested with molluscs exposed to high-CO₂ conditions. In contrast, studies of numerous vertebrate species suggest that OA can disrupt the ability of both prey and predators to detect important chemical cues (Munday *et al.*, 2009; Nilsson *et al.*, 2012; Leduc *et al.*, 2013). These examples suggest that predator preference for prey from acidified conditions may in part be due to inherent variability in their foraging strategy and ability to detect differences among prey.

Behavioral effects associated with OA are also not limited to prey species. As with prey, most research on the behavioral effects of OA on predators has thus far focused on fishes, and the effects on other non-fish predators have

yet to be determined. Emerging evidence suggests that elevated CO₂ can also reduce the ability of predatory fish to detect prey species (Cripps *et al.*, 2011), possibly through neurological pathways similar to those that disrupt chemoreception and behavior in prey. In addition, there is evidence that OA can cause an increase in the size of otoliths, important organs used to detect sounds, in fish (Checkley *et al.*, 2009; Munday *et al.*, 2011; Bignami *et al.*, 2013b). Sound detection could be magnified due to an increase in otolith size, but it is unclear whether increased sound detection improves or worsens fish's ability to detect prey (or predators). This outcome may depend on whether fish can discriminate useful sounds from background noise (Bignami *et al.*, 2013a).

Moving forward—accounting for altered interaction strength

Although coastal molluscan prey show complex responses to OA, several potential outcomes increase their susceptibility to predation. As reviewed here, the effects could include decreased shell thickness or strength, less effective inducible defenses, smaller size and reduced tissue mass, degraded immune responses, and an inability to detect or avoid predators. Moreover, higher energetic requirements for predators could further increase predation rates. In contrast, predators of coastal molluscs may also suffer reductions in size or strength, and currently little is known regarding how sensing of prey by predators might also be affected. Nevertheless, on balance we hypothesize, on the basis of the potential for many of the trade-offs of prey species to increase susceptibility to predation, that *per capita* predation rates on coastal molluscs may increase in a high-CO₂ ocean.

Theoretical models of population dynamics indicate that increased *per capita* predation rates could change the functional response of the prey population (Holling, 1966). Eventually, a reduction in the prey population due to increased *per capita* predation rates would likely support fewer predators as well. However, some of the potential responses among predators, including possible reductions in size, effectiveness of offensive weapons, or ability to detect prey, could decrease the *per capita* predation rate on calcified prey. While the emergent effects of OA on predator-prey interactions are likely to depend on the energy allocation strategy of the particular prey species and its predators, we hypothesize that increases in *per capita* predation rates on calcified molluscs may be common (Fig. 3).

A crucial element of food webs is the degree of connectedness among interacting species, which could also be affected by OA-induced shifts in predation. One aspect of connectedness is predator diet breadth. Optimal foraging theory predicts that predators act to maximize the energy consumed per unit of time. A predator's foraging strategy is

therefore based on a trade-off between the energetic content of the prey and the handling time necessary to consume it or the time it takes to find it (*i.e.*, the search time) (MacArthur and Pianka, 1966; Marten, 1973; Pyke, 1984). Because OA is likely to affect the energetic content, the handling time, and potentially the abundance of some calcified prey (*e.g.*, through reductions in survival of early life-history stages), optimal foraging theory can be used to inform hypotheses about predator-prey dynamics in a high-CO₂ world. For example, specialist predators are typically those that choose prey with high energy content despite potential trade-offs associated with longer handling times. In contrast, generalist predators will often eat more prey with lower energetic content by choosing prey with shorter handling times or limiting search time by choosing prey that are abundant. As reviewed above, it is likely that OA will lower the energetic content of some calcified prey species; whether this outcome would be detrimental for specialist predators that choose prey in order to maximize energy remains unknown. Similarly, it is unclear whether generalist predators that are able to consume a wider range of prey species could cope with altered size or energetic content of calcified prey species and would instead benefit from lower handling times due to thinner shells or reduced size among some species. Changes in cue detection could also affect search times, although the outcomes of behavioral changes are unclear because of the potential for effects on both predators and prey. A relatively robust prediction may be that both specialists and generalists will tend to exhibit increases in diet breadth under OA as energetic content decreases among some prey.

Theory predicts that energy allocation to defense against predation might also come at the expense of competitive ability (Paine, 1984; Lawler, 1989). Competitively superior species that typically allocate energy to foraging or growth over defense may become locally more abundant and thus selectively targeted or favored by predators (Werner and Anholt, 1993). Because competitively dominant species are usually highly abundant, this trait may predispose these species to higher predation pressure. This trade-off between defense and competitive ability sets the stage for keystone predation, in which predation plays a disproportionately important role in structuring a community. Depending on how species allocate energy in more acidified conditions, the competitive dynamic among species could change, with repercussions for the entire community. For example, if the competitive dominants allocate more energy to shell defense with OA, their growth rates and ability to compete for space could decrease. A reduction in the growth rates of molluscs may be especially important if they are competing for space with non-calcified species or those that are less vulnerable to the changes in carbonate chemistry (Wootton

et al., 2008). Most communities are structured by a combination of bottom-up (resources) and top-down forces (predation) (Menge, 2000). Given that OA is expected to increase the energetic demands of calcified prey, species found in resource-rich environments (*e.g.*, upwelling zones) may be better able to compensate for increased energetic demands (Thomsen *et al.*, 2013) than those in more oligotrophic, resource-poor conditions.

Conclusions

Understanding the emergent effects of environmental change on populations and communities remains a challenge due to the inherent complexity of interaction networks. Community and ecosystem shifts with ocean acidification will likely be influenced by a wide range of processes, from the potential for lower population replenishment due to reduced larval survival of some species to altered competitive dynamics among dominant space-holders. However, predator-prey interactions can be disproportionately important in regulating populations and structuring communities, and may be useful starting points for scaling-up the effects of OA on individual species to populations, communities, and ecosystems (Zarnetske *et al.*, 2012). Research concerning the effects of OA on predator-prey interactions suggests that calcified prey will likely experience trade-offs in defense, growth, and reproduction that could increase *per capita* predation rates. Experimental evidence thus far suggests that a range of responses is likely among both calcified prey and their predators, and further attention to the nuances and consequences of predator-prey interactions may provide further insight into the operation of marine communities in a high-CO₂ ocean.

Acknowledgments

This work was supported by a UC Multicampus Research Programs & Initiatives Grant and NSF grants OCE-0927255, OCE-1041089, and OCE-1220648. BMJ is grateful for funding from an NSF Graduate K-12 Fellowship Program (DGE-0841297).

Literature Cited

- Amaral, V., H. N. Cabral, and M. J. Bishop. 2012. Effects of estuarine acidification on predator-prey interactions. *Mar. Ecol. Prog. Ser.* **445**: 117–127.
- Appelhans, Y. S., J. Thomsen, C. Pansch, F. Melzner, and M. Wahl. 2012. Sour times: seawater acidification effects on growth, feeding behavior and acid-base status of *Asteria rubens* and *Carcinus maenas*. *Mar. Ecol. Prog. Ser.* **459**: 85–97.
- Appleton, R. D., and A. R. Palmer. 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. *Proc. Natl. Acad. Sci.* **85**: 4387–4391.
- Asplund, M. E., S. P. Baden, S. Russ, R. P. Ellis, N. Gong, and B. E. Hernroth. 2013. Ocean acidification and host-pathogen interactions: blue mussels, *Mytilus edulis*, encountering *Vibrio tubiashii*. *Environ. Microbiol.* doi: 10.1111/1462-2920.12307.
- Babarro, J. F., M. J. Fernández Reirez, and U. Labarta. 2008. Secretion of byssal thread and attachment strength of *Mytilus galloprovincialis*: the influence of size and food availability. *J. Mar. Biol. Assoc. UK* **88**: 783–791.
- Barton, A., B. Hales, G. G. Waldbusser, C. Langdon, and R. A. Feely. 2012. The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: Implications for near-term ocean acidification effects. *Limnol. Oceanogr.* **57**: 698–710.
- Bayne, C. J., U. K. Hahn, and R. C. Bender. 2001. Mechanisms of molluscan host resistance and of parasite strategies for survival. *Parasitology* **123**: S159–S167.
- Beck, M. W., R. D. Brumbaugh, L. Airoidi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, G. J. Edgar, B. Hancock, M. C. Kay *et al.* 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience* **61**: 107–116.
- Beniash, E., A. Ivanina, N. S. Lieb, I. Kurochkin, and I. M. Sokolova. 2010. Elevated level of carbon dioxide affects metabolism and shell formation in oysters *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* **419**: 95–108.
- Bibby, R., P. Cleall-Harding, S. Rundle, S. Widdicombe, and J. Spicer. 2007. Ocean acidification disrupts induced defences in the intertidal gastropod *Littorina littorea*. *Biol. Lett.* **3**: 699–701.
- Bibby, R., S. Widdicombe, H. Parry, J. Spicer, and R. Pipe. 2008. Effects of ocean acidification on the immune response of the blue mussel *Mytilus edulis*. *Aquat. Biol.* **2**: 67–74.
- Bignami, S., I. C. Enochs, D. P. Manzello, S. Sponaugle, and R. K. Cowen. 2013a. Ocean acidification alters the otoliths of a pantropical fish species with implications for sensory function. *Proc. Natl. Acad. Sci.* **110**: 7366–7370.
- Bignami, S., S. Sponaugle, and R. K. Cowen. 2013b. Response to ocean acidification in larvae of a large tropical marine fish, *Rachycentron canadum*. *Glob. Change Biol.* **19**: 996–1006.
- Blake, J. W. 1960. Oxygen consumption of bivalve prey and their attractiveness to the gastropod, *Urosalpinx cinerea*. *Limnol. Oceanogr.* **5**: 273–280.
- Carpenter, S. R., F. J. Kitchell, and J. R. Hodgson. 1986. Cascading trophic interactions and lake productivity. *BioScience* **35**: 634–639.
- Checkley, D. M., Jr., A. G. Dickson, M. Takahashi, J. A. Radich, N. Eisenkolb, and R. Asch. 2009. Elevated CO₂ enhances otolith growth in young fish. *Science* **324**: 1683.
- Chivers, D. P., M. I. McCormick, G. E. Nilsson, P. L. Munday, S.-A. Watson, M. G. Meekan, M. D. Michell, K. C. Corkill, and M. C. O. Ferrari. 2013. Impaired learning of predators and lower prey survival under elevated CO₂: a consequence of neurotransmitter interference. *Glob. Change Biol.* **20**: 515–522.
- Cohen, A. L., and M. Holcomb. 2009. Why corals care about ocean acidification: uncovering the mechanism. *Oceanography* **22**: 118–127.
- Connell, S. D., K. J. Kroeker, K. E. Fabricius, D. I. Kline, and B. D. Russell. 2013. The other ocean acidification problem: CO₂ as a resource among competitors for ecosystem dominance. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**: 20120442.
- Crim, R. N., J. M. Sunday, and C. D. G. Harley. 2011. Elevated seawater CO₂ concentrations impair larval development and reduce larval survival in endangered northern abalone (*Haliotis kamtschatkana*). *J. Exp. Mar. Biol. Ecol.* **400**: 272–277.
- Cripps, I. L., P. L. Munday, and M. I. McCormick. 2011. Ocean acidification affects prey detection by a predatory reef fish. *PLoS One* **6**: e22736.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**: 351–389.
- de la Haye, K. L., J. I. Spicer, S. Widdicombe, and M. Briffa. 2011.

- Reduced sea water pH disrupts resource assessment and decision making in the hermit crab *Pagurus bernhardus*. *Anim. Behav.* **82**: 495–501.
- de la Haye, K. L., J. I. Spicer, S. Widdicombe, and M. Briffa. 2012. Reduced pH sea water disrupts chemo-responsive behaviour in an intertidal crustacean. *J. Exp. Mar. Biol. Ecol.* **412**: 134–140.
- Dickinson, G. H., O. B. Matoo, R. T. Tourek, I. M. Sokolova, and E. Beniash. 2013. Environmental salinity modulates the effects of elevated CO₂. *J. Exp. Biol.* **216**: 2607–2618.
- Dixon, D. L., P. L. Munday, and G. P. Jones. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol. Lett.* **13**: 68–75.
- Domenici, P., B. Allan, M. I. McCormick, and P. L. Munday. 2012. Elevated carbon dioxide affects behavioural lateralization in a coral reef fish. *Biol. Lett.* **8**: 78–81.
- Dupont, S., and M. Thorndyke. 2012. Relationship between CO₂-driven changes in extracellular acid-base balance and cellular immune response in two polar echinoderm species. *J. Exp. Mar. Biol. Ecol.* **424–425**: 32–37.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**: 1058–1060.
- Feely, R. A., J. Orr, V. J. Fabry, J. A. Kleypas, C. L. Sabine, and C. Langdon. 2009. Present and future changes in seawater chemistry due to ocean acidification. Pp. 175–188 in *Carbon Sequestration and Its Role in the Global Carbon Cycle*, B. J. McPherson and E. T. Sundquist, eds. Geophysical Monograph Series, Vol. 183, American Geophysical Union, Washington, DC.
- Ferrari, M. C. O., M. I. McCormick, P. L. Munday, M. G. Meekan, D. L. Dixon, Ö. Lonnstedt, and D. P. Chivers. 2011. Putting prey and predator into the CO₂ equation—qualitative and quantitative effects of ocean acidification on predator-prey interactions. *Ecol. Lett.* **14**: 1143–1148.
- Ferrari, M. C. O., R. P. Manassa, D. L. Dixon, P. L. Munday, M. I. McCormick, M. G. Meekan, A. Sih, and D. P. Chivers. 2012. Effects of ocean acidification on learning in coral reef fishes. *PLoS One* **7**: e31478.
- Garrity, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* **65**: 559–574.
- Gaylord, B., T. M. Hill, E. Sanford, E. A. Lenz, L. A. Jacobs, K. N. Sato, A. D. Russell, and A. Hettinger. 2011. Functional impacts of ocean acidification in an ecologically critical foundation species. *J. Exp. Biol.* **214**: 2586–2594.
- Gazeau, F., C. Quiblier, J. M. Jansen, J. P. Gattuso, J. J. Middelburg, and C. H. R. Heip. 2007. Impact of elevated CO₂ on shellfish calcification. *Geophys. Res. Lett.* **34**: 1–5.
- Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* **25**: 325–331.
- Gooding, R. A., C. D. G. Harley, and E. Tang. 2009. Elevated water temperature and carbon dioxide concentration increase the growth of a keystone echinoderm. *Proc. Natl. Acad. Sci.* **106**: 9316–9321.
- Harley, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science* **334**: 1124–1127.
- Hernroth, B., S. Baden, M. Thorndyke, and S. Dupont. 2011. Immune suppression of the echinoderm *Asterias rubens* (L.) following long-term ocean acidification. *Aquat. Toxicol.* **103**: 222–224.
- Hettinger, A., E. Sanford, T. M. Hill, A. D. Russell, K. N. S. Sato, J. Hoey, M. Forsch, H. N. Page, and B. Gaylord. 2012. Persistent carry-over effects of planktonic exposure to ocean acidification in the Olympia oyster. *Ecology* **93**: 2758–2768.
- Hiebenthal, C., E. R. Philipp, A. Eisenhauer, and M. Wahl. 2013. Effects of seawater pCO₂ and temperature on shell growth, shell stability, condition and cellular stress of Western Baltic Sea *Mytilus edulis* (L.) and *Arctica islandica* (L.). *Mar. Biol.* **160**: 2073–2087.
- Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* **48**: 1–86.
- Hughes, R. N., and S. de B. Dunkin. 1984. Behavioral components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. *J. Exp. Mar. Biol. Ecol.* **77**: 45–68.
- Hutton, M. L., R. J. Harvey, F. G. P. Earley, E. A. Barnard, and M. G. Darlison. 1993. A novel invertebrate GABA receptor-like polypeptide: sequence and pattern in gene expression. *FEBS Lett.* **326**: 112–116.
- Ishimatsu, A., M. Hayashi, and T. Kikkawa. 2008. Fishes in high-CO₂ acidified oceans. *Mar. Ecol. Prog. Ser.* **373**: 295–302.
- Kautsky, N., K. Johannessen, and M. Tedengren. 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations: growth and morphology. *Mar. Ecol. Prog. Ser.* **59**: 203–210.
- Kim, Y., and E. N. Powell. 2007. Distribution of parasites and pathologies in sentinel bivalves: NOAA status and trends “Mussel Watch” program. *J. Shellfish Res.* **26**: 1115–1151.
- Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* **13**: 1419–1434.
- Kroeker, K. J., R. L. Kordas, R. N. Crim, I. E. Hendriks, L. Ramajo, G. G. Singh, C. Duarte, and J.-P. Gattuso. 2013a. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Glob. Change Biol.* **19**: 1884–1896.
- Kroeker, K. J., F. Micheli, and M. C. Gambi. 2013b. Ocean acidification causes ecosystem shifts via altered competitive interactions. *Nat. Clim. Change* **3**: 156–159.
- Lafferty, K. D. 1997. Environmental parasitology: what can parasites tell us about human impacts on the environment. *Parasitol. Today* **13**: 251–255.
- Landes, A., and M. Zimmer. 2012. Acidification and warming affect both a calcifying predator and prey, but not their interaction. *Mar. Ecol. Prog. Ser.* **450**: 1–10.
- Lawler, S. P. 1989. Behavioral responses to predators and predation risk in four species of larval anurans. *Anim. Behav.* **38**: 1039–1047.
- Leduc, A. O. H. C., P. L. Munday, G. E. Brown, and M. C. O. Ferrari. 2013. Effects of acidification on olfactory-mediated behaviour in freshwater and marine ecosystems: a synthesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**: 20120447.
- Leonard, G. H., M. D. Bertness, and P. O. Yund. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology* **80**: 1–14.
- MacArthur, R. H., and E. R. Pianaka. 1966. On optimal use of a patchy environment. *Am. Nat.* **100**: 603–609.
- Manríquez, P. H., M. E. Jara, M. L. Mardones, J. M. Navarro, R. Torres, M. A. Lardies, C. A. Vargas, C. Duarte, S. Widdicombe, J. Salisbury, and N. A. Lagos. 2013. Ocean acidification disrupts prey responses to predator cues but not net prey shell growth in *Concholepa concholepa* (loco). *PLoS One* **8**: e68643.
- Marten, G. C. 1973. An optimization equation for predation. *Ecology* **54**: 92–101.
- Matozzo, V., A. Chinellato, M. Munari, L. Finos, M. Bressan, and M. G. Marin. 2012. First evidence of immunomodulation in bivalves under seawater acidification and increased temperature. *PLoS One* **7**: e33820.
- McDonald, M. R., J. B. McClintock, C. D. Amsler, D. Rittschof, R. A. Angus, B. Orihuela, and K. Lutostanski. 2009. Effects of ocean acidification over the life history of the barnacle *Amphibalanus amphitrite*. *Mar. Ecol. Prog. Ser.* **385**: 179–187.
- Melzner, F., M. A. Gutowska, M. Langenbuch, S. Dupont, M. Lucasen, M. C. Thorndyke, and M. Bleich. 2009. Physiological basis for high CO₂ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* **6**: 2313–2331.

- Melzner, F., P. Stange, K. Trübenbach, J. Thomsen, I. Casties, U. Panknin, S. N. Gorb, and M. A. Gutowska. 2011. Food supply and seawater $p\text{CO}_2$ impact calcification and internal shell dissolution in the blue mussel *Mytilus edulis*. *PLoS One* 6: e24223.
- Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.* 250: 257–289.
- Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.* 51: 429–450.
- Metalunan, S., P. Calosi, S. D. Rundle, S. Widdicombe, and A. J. Moody. 2013. Effects of ocean acidification and elevated temperature on shell plasticity and its energetic basis in an intertidal gastropod. *Mar. Ecol. Prog. Ser.* 472: 155–168.
- Michaelidis, B., C. Ouzounis, A. Palaras, and H. O. Pörtner. 2005. Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.* 293: 109–118.
- Moret, Y., and P. Schmid-Hempel. 2000. Survival for immunity: the price of immune system activation for bumblebee workers. *Science* 290: 1166–1168.
- Munday, P. L., D. L. Dixon, J. M. Donelson, G. P. Jones, M. S. Pratchett, G. V. Devitsina, and K. B. Døving. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Natl. Acad. Sci.* 106: 1848–1852.
- Munday, P. L., D. L. Dixon, M. I. McCormick, M. Meekan, M. C. O. Ferrari, and D. P. Chivers. 2010. Replenishment of fish populations is threatened by ocean acidification. *Proc. Natl. Acad. Sci.* 107: 12930–12934.
- Munday, P. L., V. Hernaman, D. L. Dixon, and S. R. Thorrold. 2011. Effect of ocean acidification on otolith development in larvae of a tropical marine fish. *Biogeosciences* 8: 1631–1641.
- Nilsson, G. E., D. L. Dixon, P. Domenici, M. I. McCormick, C. Sørensen, S.-A. Watson, and P. L. Munday. 2012. Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nat. Clim. Change* 2: 201–204.
- Norberg, J., and M. Tedengren. 1995. Attack behavior and predatory success of *Asterias rubens* L. related to differences in size and morphology of the prey mussel *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 186: 207–220.
- O'Donnell, M. J., M. N. George, and E. Carrington. 2013. Mussel byssus attachment weakened by ocean acidification. *Nat. Clim. Change* 3: 587–590.
- Orr, J. C., V. J. Fabry, O. Aumont, L. Bopp, S. C. Doney, R. A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, and F. Joos. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437: 681–686.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93–120.
- Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57: 858–873.
- Paine, R. T. 1984. Ecological determinism in the competition for space. *Ecology* 65: 1339–1348.
- Palmer, A. R. 1981. Do carbonate skeletons limit the rate of body growth? *Nature* 292: 150–152.
- Palmer, A. R. 1992. Calcification in marine molluscs: how costly is it? *Proc. Natl. Acad. Sci.* 89: 1379–1382.
- Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci.* 98: 3904–3908.
- Pörtner, H. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Mar. Ecol. Prog. Ser.* 373: 203–217.
- Pressier, E. L., D. I. Bolnick, and M. F. Bernard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86: 501–509.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15: 523–575.
- Railsback, S. F., and B. C. Harvey. 2013. Trait-mediated trophic interactions: is foraging theory keeping up? *Trends Ecol. Evol.* 28: 119–125.
- Rolff, J., and M. T. Siva-Jothy. 2003. Invertebrate ecological immunity. *Science* 301: 472–475.
- Rosa, R., and B. A. Seibel. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proc. Natl. Acad. Sci.* 105: 20776–20780.
- Rossoll, D., R. Bermúdez, H. Hauss, K. G. Schulz, U. Riebesell, U. Sommer, and M. Winder. 2012. Ocean acidification-induced food quality deterioration constrains trophic transfer. *PLoS One* 7: e34737.
- Rundle, S. D., J. I. Spicer, R. A. Coleman, J. Vosper, and J. Soane. 2004. Environmental calcium modifies induced defenses in snails. *Proc. R. Soc. Lond. B Biol. Sci.* 271: S67–S70.
- Sandland, G. J., and D. J. Minchella. 2003. Costs of immune defense: an enigma wrapped in an environmental cloak? *Trends Parasitol.* 19: 571–574.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283: 2095–2097.
- Sanford, E., B. Gaylord, A. Hettinger, E. A. Lenz, K. Meyer, and T. M. Hill. 2014. Ocean acidification increases the vulnerability of native oysters to predation by invasive snails. *Proc. R. Soc. Lond. B Biol. Sci.* 281: 20132681.
- Sheldon, B. C., and S. Verhulst. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends Ecol. Evol.* 11: 317–321.
- Simpson, S. D., P. L. Munday, M. L. Wittenrich, R. Manassa, D. L. Dixon, M. Gagliano, and H. Y. Yan. 2011. Ocean acidification erodes crucial auditory behaviour in a marine fish. *Biol. Lett.* doi: 10.1098/rsbl.2011.0293.
- Stewart, P., E. A. Williams, M. J. Stewart, N. Soonklang, S. M. Degnan, S. F. Cummins, P. J. Hanna, and P. Sobhon. 2011. Characterization of a GABA_A receptor β subunit in the abalone *Haliotis asinina* that is upregulated during larval development. *J. Exp. Mar. Biol. Ecol.* 410: 53–60.
- Stumpp, M., J. Wren, F. Melzner, M. C. Thorndyke, and S. T. Dupont. 2011. CO₂ induced seawater acidification impacts sea urchin larval development. I. Elevated metabolic rates decrease scope for growth and induce developmental delay. *Comp. Biochem. Physiol. A Comp. Physiol.* 3: 331–340.
- Suchanek, T. H. 1992. Extreme biodiversity in the marine environment: Mussel bed communities of *Mytilus californianus*. *Northwest Environ. J.* 8: 150–152.
- Talmage, S. C., and C. J. Gobler. 2010. Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proc. Natl. Acad. Sci.* 107: 17246–17251.
- Talmage, S. C., and C. J. Gobler. 2011. Effects of elevated temperature and carbon dioxide on the growth and survival of larvae and juveniles of three species of northwest Atlantic bivalves. *PLoS One* 5: e26941.
- Thompson, D. J. 1975. Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *J. Anim. Ecol.* 44: 907–916.
- Thomsen, J., M. A. Gutowska, J. Saphorster, A. Heinemann, K. Trübenbach, J. Fietzke, C. Hiebenthal, A. Eisenhauer, A. Kortzinger, M. Wahl, and F. Melzner. 2010. Calcifying invertebrates succeed in a naturally CO₂-rich coastal habitat but are threatened by high levels of future acidification. *Biogeosciences* 7: 3879–3891.
- Thomsen, J., I. Casties, C. Pansch, A. Kortzinger, and F. Melzner.

- 2013.** Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. *Glob. Change Biol.* **19**: 1017–1027.
- Trussell, G. C. 1996.** Phenotypic plasticity in an intertidal snail: the role of a common crab predator. *Evolution* **50**: 448–454.
- Trussell, G. C., and M. O. Nicklin. 2002.** Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* **83**: 1635–1647.
- Tunncliffe, V., K. T. A. Davies, D. A. Butterfield, R. W. Embley, J. M. Rose, and W. W. Chadwick, Jr. 2009.** Survival of mussels in extremely acidic waters on a submarine volcano. *Nat. Geosci.* **2**: 344–348.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008.** Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**: 1351–1363.
- Vermeij, G. J. 1982.** Phenotypic evolution in a poorly dispersing snail after arrival of a predator. *Nature* **299**: 349–350.
- Vermeij, G. J. 1993.** *A Natural History of Shells*. Princeton University Press, Princeton.
- Waldbusser, G. G., E. L. Brunner, B. A. Haley, B. Hales, C. J. Langdon, and F. G. Prahl. 2013.** A developmental and energetic basis linking larval oyster shell formation to acidification sensitivity. *Geophys. Res. Lett.* **40**: 2171–2176.
- Watson, S.-A., S. Lefevre, M. I. McCormick, P. Domenici, G. E. Nilsson, and P. L. Munday. 2013.** Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels. *Proc. R. Soc. Lond. B Biol. Sci.* **281**: 20132377.
- Werner, E. E., and B. R. Anholt. 1993.** Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* **142**: 242–272.
- Wood, H. L., J. I. Spicer, and S. Widdicombe. 2008.** Ocean acidification may increase calcification rates, but at a cost. *Proc. R. Soc. Lond. B Biol. Sci.* **275**: 1767–1773.
- Wootton, J. T., C. A. Pfister, and J. D. Forester. 2008.** Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proc. Natl. Acad. Sci.* **105**: 18848–18853.
- Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012.** Biotic multipliers of climate change. *Science* **336**: 1516–1518.