

Behavioral responses to ocean acidification in marine invertebrates: new insights and future directions*

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Abstract Ocean acidification (OA) affects marine biodiversity and alters the structure and function of marine populations, communities, and ecosystems. Recently, effects of OA on the behavioral responses of marine animals have been given with much attention. While many of previous studies focuses on marine fish. Evidence suggests that marine invertebrate behaviors were also be affected. In this review, we discussed the effects of CO₂-driven OA on the most common behaviors studied in marine invertebrates, including settlement and habitat selection, feeding, anti-predatory, and swimming behaviors, and explored the related mechanisms behind behaviors. This review summarizes how OA affects marine invertebrate behavior, and provides new insights and highlights novel areas for future research.

Keyword: carbon dioxide; global climate change; invertebrate behavior; ocean acidification (OA); pH

1 INTRODUCTION

Rapid increase in atmospheric carbon dioxide (CO₂) concentration and subsequent ocean acidification (OA) have been reported for having a broad range of biological impacts on marine animals, including effects on physiology, growth and development, calcification, and overall survival (Kroeker et al., 2010, 2013 for meta-analytical reviews). More recently, behavioral consequences of OA for marine animals have been of great interest (Briffa et al., 2012; Clements and Hunt, 2015; Nagelkerken and Munday, 2016). Animal behaviors not only regulate the overall welfare and status of specific species and their populations (Sih et al., 2004), but also have a potential evolutionary ability to affect ecosystems (Fabry et al., 2008). For example, changes in foraging or feeding behavior have a certain impact on the survival and reproduction of animals, and the prey's resistance or evasion to predators can affect populations and community structures and ultimately ecosystem functions (Persons et al., 2001).

It is thus critical to understand the potential effects of global change stressors such as ocean acidification on the behavior of marine animals. Here, we provide an updated overview of the behavioral impacts of OA on the most common marine invertebrates, such as settlement and habitat selection, feeding behavior, anti-predator responses, swimming and movement, and explore the potential mechanisms behind behaviors, highlighting new insights and key directions for future research of OA and the behavior.

2 OVERVIEW OF OCEAN ACIDIFICATION ON INVERTEBRATE BEHAVIORS

Experimental evidences suggest that near-future ocean acidification can exert impacts on a number of behavioral processes that are important for growth and survival of marine invertebrates (Table 1).

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Table 1 A summary of the impacts of ocean acidification on marine invertebrate behaviors

Study	Species	pH/pCO ₂	Control pH/pCO ₂	Behaviors	Responses	Exposure time
Cnidaria						
Albright et al. (2008)	<i>Porites astreoides</i>	560, 720 µatm	380 µatm	Settlement success	-	1 week
Albright et al. (2010)	<i>Acropora palmata</i>	560, 800 µatm	400 µatm	Settlement success	-	1–6 days
Anlauf et al. (2011)	<i>Porites panamensis</i>	493, 861, 950 µatm	487 µatm	Settlement success	-	10 days
Albright and Langdon (2011)	<i>Porites astreoides</i>	560, 800 µatm	380 µatm	Settlement success	↓	24 hours
Doropoulos et al. (2012)	<i>Acropora millepora</i>	807, 1 299 µatm	401 µatm	Settlement success	↓	6 days
Doropoulos and Diaz-Pulido (2013)	<i>Acropora selago</i>	705, 1 214 µatm	447 µatm	Settlement success	↓	3 days
Webster et al. (2013)	<i>Hydrolithon onkodes</i>	822, 1 187, 1 638 µatm	464 µatm	Settlement success	↓	6 weeks
Viyakarn et al. (2015)	<i>Pocillopora damicornis</i>	pH 7.6, 7.9	pH 8.1	Settlement success	↓	24 hours
Annelida						
Widdicombe and Needham (2007)	<i>Nereis virens</i>	pH 5.6, 6.5	pH 7.3	Burrowing	-	5 weeks
Bryozoa						
Pecquet et al. (2017)	<i>Bugula neritina</i>	pH 7.6, 7.9	pH 8.1	Time to settle	↓	6 hours
Arthropoda						
De La Haye et al. (2011)	<i>Pagurus bernhardus</i>	pH 6.8	pH 8.2	Shell detection Antennular flicking	- ↓	5 days
Dissanayake and Ishimatsu (2011)	<i>Metapenaeus joyneri</i>	1 kPa	0.04 kPa	Swimming	↓	10 days
Alenius and Munguia (2012)	<i>Paradella diana</i>	pH 7.6 stable pH 7.6 variable	pH 8.1	Swimming	- ↓	22 days
Appelhans et al. (2012)	<i>Carcinus maenas</i>	1 120 µatm 4 000 µatm	650 µatm	Feeding	- ↓	10 weeks
De La Haye et al. (2012)	<i>Pagurus bernhardus</i>	pH 6.8	pH 8.2	Foraging Movement	↓	5 days
Li and Gao (2012)	<i>Centropages tenuiremis</i>	1 000 µatm	390 µatm	Feeding rates	↑	4 days
Landes and Zimmer (2012)	<i>Carcinus maenas</i>	pH 7.7	pH 8.0	Prey handling time	-	5 months
Saba et al. (2012)	<i>Euphausia superba</i>	672×10 ⁻⁶	581×10 ⁻⁶	Feeding rate	↓	48 hours
Zittier et al. (2013)	<i>Hyas araneus</i>	750, 1 120, 3 000 µatm	380 µatm	Self-righting	↑	12 days
Christmas (2013)	<i>Metacarcinus (Cancer) magister Hemigrapsus oregonensis</i>	1 000×10 ⁻⁶	400×10 ⁻⁶	Feeding rate Swimming behavior	- -	1-5 days
Kim and Barry (2016)	<i>Pagurus tanneri</i>	pH 7.1	pH 7.6	Anti-predation behavior	-	4 weeks
Benítez et al. (2016)	<i>Orchestoidea tuberculata</i>	1 000 µatm	390 µatm	Food selectivity	↓	4 days
Duarte et al. (2016)	<i>Orchestoidea tuberculata</i>	1 000 µatm	390 µatm	Food selectivity	↓	10 days
Schram et al. (2017)	<i>Gondogeneia antarctica</i>	pH 7.6	pH 8.0	Food selectivity	-	39 days
Glaspie et al. (2017)	<i>Callinectes sapidus</i>	pH 7.2	pH 7.8	Handling time Search time	- -	30 days
Wu et al. (2017)	<i>Charybdis japonica</i>	pH 7.3	pH 8.1	Foraging time Feeding time	↓ ↓	48 hours
Wang et al. (2018)	<i>Cancer pagurus</i>	1 200 2 300 µatm	390 µatm	Feeding behavior Food selectivity	↓ ↓	4 weeks
Mollusca						
Bibby et al. (2007)	<i>Littorina littorea</i>	pH 6.63	pH 7.97	Predator avoidance	↑	15 days
Ellis et al. (2009)	<i>Littorina obtusata</i>	pH 7.6	pH 8.1	Spinning rate Crawling Periodization	↓ ↓	24 days
Green et al. (2009)	<i>Mya arenaria</i>	pH 7.32	Not reported	Settlement	↓	30 days
Amaral et al. (2012)	<i>Saccostrea glomerata</i>	pH 7.72	pH 6.52	Food selectivity	↓	10 days
Schalkhauser et al. (2013)	<i>Pecten maximus</i>	0.112 kPa	0.040 kPa	Clapping amount Clapping force	- ↓	60 days

References cited in the table were selected based on the marine invertebrate behavioral responses to ocean acidification in about past 10 years. Such behavioral responses include settlement, burrowing, swimming, foraging, anti-predation, and other relevant behaviors that marine invertebrates possess to respond to ocean acidification. The responses are classified in taxon order. ↑ indicates a positive response; ↓ indicates a negative response; - indicates no effect. Ω: carbonate (aragonite) saturation state.

To be continued

Table 1 Continued

Study	Species	pH/pCO ₂	Control pH/pCO ₂	Behaviors	Responses	Exposure time
Mollusca						
Green et al. (2013)	<i>Mercenaria mercenaria</i>	Ω: 0.68	Not reported	Burrowing	↓	30 days
Vargas et al. (2013)	<i>Concholepas concholepas</i>	700, 1 000×10 ⁻⁶	400×10 ⁻⁶	Feeding	↓	6–8 weeks
Manríquez et al. (2013)	<i>Concholepas concholepas</i>	716, 1036 μatm	388 μatm	Self-righting behavior	↓	83 days
Manríquez et al. (2014)	<i>Concholepas concholepas</i>	1400 μatm	500 μatm	Dislodgement resistance	↑	5.8 months
Clements and Hunt (2014)	<i>Mya arenaria</i>	Ω: 0.05–1.05	Not reported	Burrowing	↓	2 hours
				Dispersal	↑	
Sanford et al. (2014)	<i>Urosalpinx cinerea</i>	1000 μatm	500 matm	Drilling predation	-	20 days
Spady et al. (2014)	<i>Idiosepius pygmaeus</i>	626, 956 μatm	447 μatm	Swimming	↑	5 days
Vargas et al. (2015)	<i>Concholepas concholepas</i> <i>Perumytilus purpuratus</i>	700, 1 000 μatm	400×10 ⁻⁶	Feeding rate	↓	6–8 weeks
				Feeding	↓	
Watson et al. (2014)	<i>Gibberulus gibberulus</i> <i>gibbosus</i>	961 μatm	405 μatm	Predator escape (jumping adult)	↓	5-7 days
				Predator escape (non-jumping adult)	↑	
				Activity (speed)	↓	
Queirós et al. (2015)	<i>Nucella lapillus</i>	750, 1 000×10 ⁻⁶	380×10 ⁻⁶	Foraging time	↓	14 months
				Foraging distance	↓	
				Prey handling time	↓	
Sui et al. (2015)	<i>Mytilus coruscus</i>	pH 7.3, 7.7	pH 8.1	Byssus threads diameter	↓	72 hours
				Byssus secretion rate	↓	
Li et al. (2015)	<i>Mytilus coruscus</i>	pH 7.4, 7.7	pH 8.1	Frequency of shed byssus	↓	3 days
				Byssus length	↓	
				Handling time	↓	
Dupont et al. (2015)	<i>Brachidontes pharaonic</i>	pH 7.5	pH 8.0	Handling time	↓	4 weeks
Jellison et al. (2016)	<i>Tegula funebris</i>	pH 6.4–8.0	Not reported	Refuge time	↓	5 days
Bergan et al. (2017)	<i>Limacina retroversa</i>	800, 1 200 μatm	400 μatm	Sinking speed	↓	4 weeks
Domenici et al. (2017)	<i>Concholepas concholepas</i>	1 400 μatm	500 μatm	Movement duration	↓	6 months
				Decision-making time	↓	
Xu et al. (2017)	<i>Thais clavigera</i>	950, 1 250 μatm	380 μatm	Prey handling time	↓	
Maboloc and Chan (2017)	<i>Crepidula onyx</i>	pH 7.3, 7.7	pH 8.1	Settlement success	-	14 days
Watson et al. (2017)	<i>Conus marmoreus</i>	975 μatm	390 μatm	Predation rate	↓	32 hours
Wright et al. (2018b)	<i>Tenguella marginalba</i>	909 μatm	481 μatm	Consumption rate	↑	6 weeks,
Benítez et al. (2018)	<i>Choromytilus chorus</i>	750, 1 200 μatm	500 μatm	Feeding behavior	-	30 days
Spady et al. (2018)	<i>Idiosepius pygmaeus</i>	737, 934 μatm	438 μatm	Predation rate	↓	5 days
	<i>Sepioteuthis lessoniana</i>	935 μatm	435 μatm	Striking distance	↓	
Echinodermata						
Havenhand et al. (2008)	<i>Heliocidaris erythrogramma</i>	pH 7.7	pH 8.1	Swimming speed	↓	Not reported
Chan et al. (2011)	<i>Dendraster excentricus</i>	1 000×10 ⁻⁶	380×10 ⁻⁶	Swimming	-	10 hours
Appelhans et al. (2012)	<i>Asterias rubens</i>	1 250, 3 500 μatm	650 μatm	Feeding rates	↓	10 weeks
Burnell et al. (2013)	<i>Amblypneustes pallidus</i>	pH 7.9	pH 8.1	Grazing	↑	5 days
Uthicke et al. (2013)	<i>Acanthaster planci</i>	pH 7.6, 7.9	pH 8.1	Settlement	↓	86 days
Appelhans et al. (2014)	<i>Asterias rubens</i>	1 120, 4 000 μatm	390×10 ⁻⁶	Feeding rates	↓	6–39 weeks
				Self-righting	-	
Barry et al. (2014)	<i>Strongylocentrotus fragilis</i>	3 255×10 ⁻⁶	1 028×10 ⁻⁶	Movement	-	27 days
				Foraging	↓	
Chan et al. (2015)	<i>Strongylocentrotus purpuratus</i>	pH 7.2, 7.6	pH 8.0	Swimming speed	-	13 days
Chan et al. (2016)	<i>Amphiura filiformis</i>	pH 7.3, 7.7	pH 8.0	Swimming speed	↓	7 days
García et al. (2018)	<i>Paracentrotus lividus</i>	pH 7.7	pH 8.1	Settlement success	↓	7 days

2.1 Settlement and habitat selection

Most marine invertebrates have a planktonic larval stage. When competent, they settle and metamorphose, switching from a pelagic to benthic lifestyle. This transitional period has a significant impact on the population dynamics and community structure, as successful settlement is necessary for population recruitment (Rodríguez et al., 1993; Caley et al., 1996). Suitable habitat selection and the avoidance of predators are key for at-settlement and post-settlement success (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). Thus, larvae not only need to locate suitable benthic habitats properly, but also must assess the environmental quality in order to choose an ideal habitat (Igulu et al., 2011, 2013). To do this, settling invertebrate larvae make use of olfactory and visual functions to detect environmental cues and select suitable habitats during settlement (Huijbers et al., 2012). However, different sense functions may exhibit different sensitivities to elevated CO₂. For example, animals using visual cues for settlement may be significantly affected by elevated CO₂ (Ferrari et al., 2012). Some animals using visual or other perceptual pathways can compensate for diminished olfactory ability under elevated CO₂ (Devine et al., 2012). Those differential sensitivities may be a compensatory mechanism to overcome effects of OA on settlement. Moreover, during larval settlement, some species using multiple sensory pathways to detect and choose habitat have been proved less susceptible to OA effects than the species using a single sensory pathway.

OA can also have indirect effects on invertebrate settlement. For example, OA can affect metamorphosis and settlement of coral larvae by affecting the symbiosis of corals and microorganisms (Webster et al., 2013). Nakamura et al. (2011) reported that metamorphosis in the coral *Acropora digitifera* was hindered under OA conditions, and the delayed metamorphosis indirectly affected coral settlement and recruitment, despite sustained larval survival. In addition to coral settlement, OA has also been reported to alter the settlement behavior of other invertebrates as well, including marine molluscs, echinoderms, foraminifera, nematodes, polychaetes, crustaceans, and chaetognaths (Cigliano et al., 2010; Uthicke et al., 2013; Maboloc and Chan, 2017; Pecquet et al., 2017; García et al., 2018). Additionally, recent evidences suggest that OA can alter biogenic habitat (created by plants and animals), which can affect the composition of settlement cues and potentially reduce

the availability of suitable settlement habitat (Uthicke et al., 2013; Sunday et al., 2017). However, much more work is needed to determine how the combined direct (e.g. sensory interference) and indirect (e.g. delayed metamorphosis, alteration of biogenic habitat, etc.) effects of elevated CO₂ act to alter settlement behavior in marine invertebrates.

2.2 Feeding behavior

Food provides the necessary energy to carry out functions for life. Experimental evidences suggest that elevated CO₂ can affect the ability of marine invertebrates to feed, although effects are variable. For example, Christmas (2013) reported that there was no significant difference in feeding rates of either the dungeness crab *Metacarcinus magister* or the Pacific green shore crab *Hemigrapsus oregonensis* larvae between the CO₂ treatments. The predation success rate of the predatory sea snail *Conus marmoreus* on the tropical conch *Gibberulus gibberulus gibbosus* was reported to be negatively affected by elevated CO₂, as predation rates decreased by ~50% under acidification (Watson et al., 2017). The predatory muricid gastropods *Morula marginalba* consumed higher amount of oysters *Saccostrea glomerata* from elevated CO₂ estuarine sites than oysters from reference sites (Amaral et al., 2012). In a predator-prey system containing mussels *Brachidontes pharaonic* (prey) and predatory crabs *Eriphia verrucosa*, Dupont et al. (2015) showed that handling time of the crabs was significantly reduced by ~27% when feeding on mussels from elevated CO₂ conditions. Xu et al. (2017) found that the prey handling time of the muricid gastropod *Thais clavigera* on the mussel *Brachidontes variabilis* was decreased significantly while the prey consumption rate was independent of pCO₂ levels, although the prey searching time was increased significantly at elevated pCO₂. These findings indicated that the predator-prey interaction between *T. clavigera* and *B. variabilis* was altered under OA, which may have a long-term impact on the population dynamics of the interspecific interaction. However, Glaspie et al. (2017) found that the handling time and search time for the crab *Callinectes sapidus* preying on clams was not impacted by the acidified treatment. Recent evidences emphasized that the ecological outcomes of predator-prey interactions are dependent on the effects of elevated CO₂ on both the predator and the prey (Kroeker et al., 2014 for detailed examples). The potential for near-future OA to affect such nuanced

ecological interactions requires further research.

Other than active foraging, filter feeding is a quite typical feeding behavior of many sessile invertebrates such as bivalve mollusks. Recent studies have reported that OA could negatively affect the feeding of bivalves. For example, Zhao et al. (2017a) demonstrated that clearance rate of the blood clam *Tegillarca granosa* was significantly suppressed by OA treatment, indicating the feeding activity of the clam was impaired under OA scenarios. In addition, after exposure to OA, the mussel *Mytilus coruscus* would reduce the feeding rate (Wang et al., 2015), and the Manila clam *Ruditapes philippinarum* would decrease the food uptake (Xu et al., 2016). The impaired feeding activity may reduce the energy uptake from food sources, influence the growth and reproduction of these organisms, and ultimately have population and community consequences.

Wu et al. (2017) reported that food selectivity of Japanese shore crab *Charybdis japonica*, was unaltered by elevated CO₂, while foraging and feeding time were increased under elevated CO₂, and the same situation was also found in the brown crab *Cancer pagurus* (Wang et al., 2018). The lack of selectivity effect may have resulted from that the weaker periwinkle shell under OA offsets the weaker crab claw on crushing prey (Landes and Zimmer, 2012). Wright et al. (2018a) demonstrated that the endemic whelk *Tenguella marginalba* showed no preference between native preys (the Sydney rock oyster *Saccostrea glomerata* and the mussel *Trichomya hirsuta*) and invasive Pacific oyster *Crassostrea gigas*. However, when both oysters and whelks were kept under elevated pCO₂, the whelk *T. marginalba* consumed more oysters *C. gigas* than *S. glomerata* (Wright et al., 2018b). Elevated pCO₂ may increase the energy requirements of the predatory whelks to maintain homeostasis, and thus the prey consumption by the predator increased (Wright et al., 2018b). Under acidification conditions, the nutritional quality of the brown alga *Durvillea antarctica* was decreased, and the amphipod *Orchestoidea tuberculata* showed lower preference for these algae compared with normal *D. antarctica* (Duarte et al., 2016). However, this amphipod grazed more OA exposed algae compared with normal *D. antarctica* under no-food choice conditions (Duarte et al., 2016). In a later study, both juvenile and adult *O. tuberculata* consumed more algae cultured under normal pH than algae cultured under low pH when there was a food choice (Benítez et al., 2016). However, when they

were fed with only one type algae (i.e. no food choice), juveniles consumed significantly more algae exposed to low pH compared with algae cultured under normal pH, while adults consumed more algae maintained at normal pH level (Benítez et al., 2016). These results highlight the effects of OA on algae and subsequently the ontogenetic variability (i.e. juvenile and adult) in the feeding behavior of amphipods.

Altered feeding behaviors have been investigated, and some potential mechanisms need to be assessed. For example, neurological function has been linked to ciliary beating in marine bivalves, which is an important behavior in bivalve feeding. More specifically, serotonin and dopamine have been linked to ciliary beating in the gills of bivalve molluscs and GABA plays a major inhibitory role in regulating the actions of serotonin on ciliary beating (e.g., Catapano et al., 1978, 1979, 2016; Carroll et al., 2007). The elevated CO₂ is known to influence neurological function (GABA_A receptor functioning and associated behaviors) in marine invertebrates (Watson et al., 2014; Clements et al., 2017), neurological effects of elevated CO₂ may affect ciliary beating and thus alter filter feeding behavior. Given the likelihood that numerous mechanistic drivers may act to alter invertebrate feeding behavior under elevated CO₂, future studies would benefit from teasing out the respective contributions of mechanistic CO₂ effects to better understand how elevated CO₂ affects different modes of feeding at multiple life history stages in a wide range of invertebrate taxa.

2.3 Anti-predatory behavior

Anti-predatory defenses are the reactions that prey produced when they detected the predation risk (Smee and Weissburg, 2016). These responses are very individual for different species. Of the current review, 53% of the relevant anti-predator behaviors showed negative responses to OA. Anti-predator escape responses of the gastropod *Gibberulus gibberulus gibbosus*, which has a strong foot to escape predators by jumping, were impaired under elevated pCO₂ as the number of leaping individuals halved and the jumping latency increased (Watson et al., 2014). Under elevated CO₂, self-righting (i.e., re-orientation after dislodgement) time was doubled in the Chilean abalone *Concholepas concholepas* in the presence of the predatory crab *Acanthocyclus hassleri* (Manríquez et al., 2013). The ability to escape from predators in this abalone had also been reported to decrease under elevated CO₂ (Manríquez et al., 2014). Defensive

behaviors in response to visual predator cues in the squid *Idiosepius pygmaeus* can be impacted by low pH, as activity levels increased by 19%–25%, movement (number of line crosses) increased three-fold, and the possibility of activating inkjet defense strategy had a two-fold increase under elevated CO₂ conditions (Spady et al., 2014). Byssus thread, a proteinous material, is secreted by the byssal gland at the base of the foot of mussels for anchorage on hard substratum. Enhanced byssus production can reduce the probabilities of being dislodged from the substratum and consumed by their predators. It serves as anti-predatory responses when mussels are exposed to predators. The number of byssus (attachment threads) produced by the mussel *Mytilus coruscus* was found to decrease under low pH (Sui et al., 2015), it may be explained by the decreased byssus-associated proteins (Sui et al., 2017). Both mechanical performance (such as strength and extensibility) and the numbers of byssal threads produced by *M. coruscus* were significantly reduced by OA (Zhao et al., 2017b). However, the presence of predators *Charybdis japonica* resulted in an increase in byssus production for *M. coruscus*, indicating that enhanced anti-predation ability occurred under elevated CO₂ when there is a threat of predation (Li et al., 2015). Ocean acidification is also reported to negatively influence morphological defenses in the form of shell thickness. The intertidal gastropod *Littorina littorea* can produce thicker shells in response to predation of crab, but this response was limited at low pH (Bibby et al., 2007). At the same time, *L. littorea* also increase avoidance behavior (percentage of time a snail spent above or at the water surface in trials) to response to the stress (Bibby et al., 2007). A recent study has found elevated pCO₂ did not affect the ability of whelks *Tenguellia marginalba* to detect a predator, although there were significant effects on their anti-predatory defense including a reduction in growth and the time spent in refuge (Jellison et al., 2016). In the case of adult deep-sea hermit crab *Pagurus tanneri*, the time taken to re-emerge from shells after a simulated predatory attack was not influenced by OA (Kim and Barry, 2016). Self-righting in adult toad crab *Hyas araneus* was unaffected by elevated CO₂ conditions (Zittier et al., 2013). Similar results were also found in juvenile sea star *Asterias rubens* (Appelhans et al., 2014). These above results suggest that ontogeny may play a key role in behavioral effects, whereby adults and juveniles are likely more tolerant to elevated CO₂ conditions than larvae.

2.4 Movement and swimming behavior

The population dynamics of marine invertebrate species is largely influenced by dispersion, movement and pre-and-post settlement (the periods before and after initial settlement through to adulthood, Pilditch et al. 2015), and the behaviors enumerated above have been reported to be affected by elevated CO₂. For example, Domenici et al. (2017) found that the keystone gastropod *Concholepas concholepas* would increase the movement duration and decision-making time under elevated pCO₂ conditions, while Manríquez et al. (2016) demonstrated this kind of gastropod was nearly still under high pCO₂ conditions, possibly by reducing metabolic activity to meet the high energy requirements associated with attachment.

Larval swimming speed in the two crabs, *Metacarcinus magister* and *Hemigrapsus oregonensis*, appeared to increase under elevated CO₂ (Christmas, 2013). Under elevated CO₂, the swimming speed of brittle star *Amphiura filiformis* larvae was reduced (Chan et al., 2016), but the purple sea urchin *Strongylocentrotus purpuratus* larvae appeared to be unaffected (Chan et al., 2015). The observed differences between species may be related to pre-exposure in their natural habitats, as *A. filiformis* naturally resides in stable environmental pH conditions, while *S. purpuratus* tend to live in the upwelling region (Droebak, Norway) where low pH may occur (Chan et al., 2015). Although the effects of near-future OA on the swimming behavior of larval invertebrates have been documented, few studies have taken into account such effects on larval dispersal (but see Chan et al., 2015). Coupled with larval development rates, the direction and speed of larval movements can influence where a given larva ends up after it is released into the water column. It is difficult to measure directly larval dispersal models incorporating larval development and mortality rates, active larval movements, and local hydrodynamics can provide a useful tool to estimate the dispersal potential of larvae (Quinn, 2014). Given that elevated CO₂ can have impacts on the movement behavior of marine invertebrates, as well as larval mortality and development (Dupont et al., 2008; Brennand et al., 2010), studies assessing the ecological effects of acidification would benefit from incorporating these effects into larval drift/dispersal models to better understand the effects of near-future acidification on dispersal potential and population connectivity. Furthermore, such studies should take local adaptation

into account (Vargas et al., 2017), as the environmental conditions at a given source can determine the impact of climate change stressors on larval development and subsequent dispersal (Quinn and Rochette, 2015).

Given that sperm can actively swim and seek out an egg, they can be considered to be engaging in an active behavior (Elgeti et al., 2015). In the context of OA, a number of studies have reported that the swimming behavior of marine invertebrate spermatozoa can be altered by elevated CO₂. Schlegel et al. (2015) observed the sea urchin *Centrosteanus rogersii* sperm motility was slightly altered by OA. Sperm motility and velocity in the crown-of-thorns starfish *Acanthaster planci* has also been reported to decrease under elevated CO₂, and the subsequent fertilization rate was decreased (Uthicke et al., 2013). OA also negatively influenced the sperm motility of the blood clam *Tegillarca granosa* (Shi et al., 2017a, b). The percentage of active spermatozoa and swimming speed of sea urchin *Heliocidaris erythrogramma* was decreased significantly at pH 7.80, and the fertility success rate was 24% lower than the normal pH 8.10 (Havenhand et al., 2008). However, it has been reported that the sperm motility rate of mussel *Mytilus galloprovincialis* significantly increased under elevated CO₂ (Eads et al., 2016). Also no significant difference in sperm motility and viability of *Crassostrea gigas* was observed between OA (pH 7.80) and control (pH 8.15) conditions (Havenhand and Schlegel, 2009). Sinking is used by pteropod for predator evasion, and altered speeds and increased visibility could increase the susceptibility of pteropods to predation. Bergan et al. (2017) found that sinking speeds were significantly slower for the pteropod *Limacina retroversa* exposed to OA in comparison to the ambient pH.

Migratory behaviors in many marine animals are often driven by sensory perception (Lohmann et al. 2008; Charpentier and Cohen, 2016). While long-distance migrations are less common in marine invertebrates, invertebrate species can exhibit regular and predictable migratory behaviors. For example, larval invertebrates often exhibit diel vertical migrations in the water column, which can serve to avoid predation while maintaining metabolic function (Ohman et al., 1983). Alongside vertical migrations, some benthic invertebrates undergo larger-scale migrations as well. These processes are difficult to quantify, and emerging technologies are making them possible to be tested regarding larger-scale invertebrate migrations under elevated CO₂ conditions. For

example, satellite tags can document large-scale movements in situ (González-Gurriarán et al., 2002; Morse and Rochette, 2016). The direct effect of acidification on an individual's ability to perceive cues could be tested by rearing animals under elevated CO₂ conditions in the lab, releasing them into the field, and tracking their movements over time. Acoustic telemetry can also be used to understand other behaviors of juvenile and adult invertebrates, such as the sheltering behavior, diel movement and activity patterns (e.g., Morse and Rochette, 2016).

3 THE MECHANISMS BEHIND BEHAVIORS

Sensory impairment under elevated CO₂ has been observed in an array of marine invertebrates, and has been identified as a vulnerable biological attribute to near-future OA (Briffa et al., 2012; Clements and Hunt, 2015; Ashur et al., 2017). Indeed, many of the behavioral effects of elevated CO₂ on marine invertebrates described above are a direct consequence of sensory impairment. Sensory systems are critical for animals to perceive their external environment. For example, chemoreception (organismal response to chemical stimuli; e.g., taste, smell) relies on both an animal's ability to receive and interpret stimuli, as well as the particular chemical composition of a given cue. In this sense, elevated CO₂ can exert morphological or chemical effects on the sensory organs of a given organism (Tierney and Atema, 1988). Additionally, elevated CO₂ may affect some aspect of the chemical structure of a cue. While the former remains undescribed, the latter has been reported in a single study for signaling molecules associated with chemosensory behavior in the crab *Carcinus maenas*, whereby elevated CO₂ altered the charge, electrostatic properties, and physical composition of three peptide signaling molecules, and that a higher cue concentration was subsequently required to elicit a behavioral response from crabs (Roggatz et al., 2016). Interestingly, physiological alterations under elevated CO₂ play less of a role than cue alterations in driving crab behavior. Ultimately, more work is required to understand the independent and combined effects of CO₂ on sensory organs and production and transmission of chemical cues.

Although alterations to sensory organs and chemical cues may affect marine invertebrate capacity to engage in sensory perception under elevated CO₂ condition, neurological (particularly GABA_A neuroreceptor interference) has been given far more

attention. GABA is the primary inhibitory neurotransmitter found in the nervous systems of vertebrates (central and peripheral) and some invertebrates (peripheral) (Jessen et al., 1979; Lunt, 1991), and the GABA_A neuroreceptor has a specific conductance for chloride (Cl⁻) and bicarbonate (HCO₃⁻) ions. During periods of environmental stress that can invoke acidosis, GABA_A neuroreceptors have reversing ability to maintain internal acid-base balance and thus proper cellular and physiological functioning (Boron, 1987; Widdicombe and Spicer, 2008). When GABA binds to the GABA_A receptor under optimal conditions, the ionic gradient at the receptor is such that Cl⁻ and HCO₃⁻ ions flow into the cell, thus preventing depolarization and resulting in a negative membrane potential and reduced neural activity (Nilsson et al., 2012). Under elevated CO₂, however, HCO₃⁻ are accumulated and Cl⁻ are pumped out of the cell in order to maintain acid-base balance and avoid acidosis, ultimately resulting in an outflow (rather than an inflow) of ions (Heuer and Grosell, 2014). This reversed ionic gradient can potentially lead to membrane depolarization, neural pathway excitation, and altered behavior.

Treating animals with gabazine provides a simple and elegant method to determine whether or not GABA_A interference acts as the mechanism behind CO₂-associated behavioral impairments. The gabazine method has been used in a number of marine fishes (Nilsson et al., 2012; Hamilton et al., 2013; Chivers et al., 2014; Chung et al., 2014; Lai et al., 2015; Ou et al., 2015); however the role of GABA_A interference in driving invertebrate behavioral responses to elevated CO₂ is less well known. In a pioneering study using an epifaunal snail, Watson et al. (2013) reported that gabazine-treated individuals reared under elevated CO₂ conditions exhibited predator avoidance behaviors on par with those of individuals reared under control CO₂ conditions. Clements and Hunt (2017) reported that gabazine-treated clams *Mya arenaria* burrowed into acidified sediments in proportions similar to control sediments, while gabazine-untreated clams showed reduced burrowing proportions in acidified sediments. Similar results also appeared in the razor clam *Sinonovacula constricta* (Peng et al., 2017). Ren et al. (2018) showed GABA expression of the larval crab *Portunus trituberculatus* was upregulated after OA exposure. Be accompanied, are anxiety-like behaviors, such as the increased average speed, preference for dark environment and fast exploration (Ren et al., 2018).

Charpentier and Cohen (2016) indicated that for Asian shore crab *Hemigrapsus sanguineus* larvae, GABA receptor might not dominate pH effects to sensation and behavior. The above results indicate that GABA might be involved in the interactions of GABA receptors and elevated-CO₂ in seawater, but further studies on GABA acting mechanism in marine animals are needed for clarification.

Alternatively, CO₂ may have negatively affected sensory processes through other pathways than the GABAergic. Alongside sensory impairment, alterations to morphological structures associated with elevated CO₂ can affect marine invertebrate behaviors. As mentioned previously, the effects of elevated CO₂ on the feeding structures of predators (e.g. crab claws, snail radulas) and the defence structures of prey (e.g. shell thickness, foot musculature) can interact in complex ways to determine the outcome of predator-prey interactions (Landes and Zimmer, 2012; Sanford et al., 2014). Such morphological changes can also affect other behaviors that have gone largely ignored in the OA literature, such as inter- and intra-specific contests/ conflicts. Shell deformation in larval bivalves may also hinder proper feeding under elevated CO₂ (Talmage and Gobler, 2010; Gray et al., 2017). Although effects of CO₂ stress on cellular function may also drive differences in feeding rates, some behavioral changes can be adaptive. For example, sea urchin larvae *Strongylocentrotus droebachiensis* exposed to elevated CO₂ expressed a high level of morphological plasticity associated with changes in swimming behavior (Chan et al., 2015), implying changes in swimming biomechanics despite a delay in development due to increased physiological costs. The above observations highlight a strong evolutionary pressure to maintain swimming in a varying environment.

4 MOVING FORWARD

The existing studies have largely confirmed the effects of acidification on marine invertebrate behaviors, although significant knowledge gaps remain. Based on recent advances, we suggest that future studies streamline efforts toward a number of key questions including (i) multiple sensory pathways (e.g., the effects on GABA_A, chemical composition of cues, and sensory organs and structures); (ii) the ecological outcomes of behaviors such as feeding (i.e., predator-prey interactions and other feeder-food systems) in which both the feeder and the food are

reared under elevated CO₂; (iii) a range of different feeding behaviors (e.g. involving ciliary action); (iv) larval dispersal and invertebrate movements. As highlighted in previous reviews, our current understanding of the OA effects on invertebrate behavior relies heavily on laboratory experiments, and constant acidification was usually chosen to conduct the environment. However, in the field, seawater pH tends to be fluctuated; current research method may not reflect the actual environment appropriately. Technologies such as electronic tagging, telemetry, and hall effect sensors can enable a shift from observing behavior in the lab to the field. Finally, studies incorporating multiple stressors, natural variability, and potential evolutionary effects (i.e., transgenerational and local acclimation and adaptation) will substantially increase predictive power with respect to understanding marine invertebrate behavior and associated ecological functioning under projected future ocean conditions.

5 DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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