

REVIEW

Marine animal behaviour in a high CO₂ ocean

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ABSTRACT: Recently, the effects of ocean acidification (OA) on marine animal behaviour have garnered considerable attention, as they can impact biological interactions and, in turn, ecosystem structure and functioning. We reviewed current published literature on OA and marine behaviour and synthesize current understanding of how a high CO₂ ocean may impact animal behaviour, elucidate critical unknowns, and provide suggestions for future research. Although studies have focused equally on vertebrates and invertebrates, vertebrate studies have primarily focused on coral reef fishes, in contrast to the broader diversity of invertebrate taxa studied. A quantitative synthesis of the direction and magnitude of change in behaviours from current conditions under OA scenarios suggests primarily negative impacts that vary depending on species, ecosystem, and behaviour. The interactive effects of co-occurring environmental parameters with increasing CO₂ elicit effects different from those observed under elevated CO₂ alone. Although 12% of studies have incorporated multiple factors, only one study has examined the effects of carbonate system variability on the behaviour of a marine animal. Altered GABA_A receptor functioning under elevated CO₂ appears responsible for many behavioural responses; however, this mechanism is unlikely to be universal. We recommend a new focus on determining the effects of elevated CO₂ on marine animal behaviour in the context of multiple environmental drivers and future carbonate system variability, and the mechanisms governing the association between acid-base regulation and GABA_A receptor functioning. This knowledge could explain observed species-specificity in behavioural responses to OA and lend to a unifying theory of OA effects on marine animal behaviour.

KEY WORDS: Animal behaviour · Carbon dioxide · Climate change · Marine ecology · Ocean acidification · Ocean climate

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INTRODUCTION

Animal behaviour contributes significantly to understanding the overall welfare and status of a particular species or population (Gonyou 1994, Sih et al. 2004) and can indicate environmental conditions and animal welfare in both laboratory and natural settings (e.g. Mench 1998). Animal behaviour also has potential evolutionary and ecological consequences. For example, predator avoidance by prey and other associated behaviours (e.g. locomotion and learning) can influence prey species survival (e.g. Brodie Jr. et al. 1991). Shifts in feeding behaviour can

also change predator survival and persistence (e.g. Persons et al. 2001). Behaviours such as feeding and predator avoidance can change population and community structure, and ultimately ecosystem functioning. For example, environmental contamination can suppress feeding behaviour and predator avoidance by prey in fishes and can change predator–prey interactions, having implications for contaminant transfer through a food web (Weis et al. 2001). Hindered prey detection could also alter optimal foraging in a wide range of species (e.g. Malmros 2012).

Many factors can influence animal behaviour. Internal physiological and biochemical processes pri-

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marily drive some behaviours, while external environmental processes drive others (e.g. Hughes 1988), such as thermoregulation in birds (e.g. Luskick et al. 1978) and predator avoidance in fish (e.g. Gregory 1993). The interactive influence of both internal and external processes, however, influences most behaviours because external environmental conditions can trigger internal sensory processes and lead to a particular behaviour (Mench 1998, Breed & Sanchez 2010). These examples illustrate the importance of knowing the internal and external processes that drive animal behaviour and understanding how changes in such processes influence behaviour.

Climate change has attracted increasing attention as an external physiological and behavioural driver. In marine systems, climate change, predominantly driven by increased anthropogenic CO₂ in the atmosphere, can affect animal behaviour through 2 primary environmental changes: (1) ocean warming in conjunction with an increasingly warming planet, and (2) increasing oceanic CO₂ concentrations and the resultant shift in pH to more acidic conditions. Though scientists have long recognized global warming and its potential impact on animal behaviour (e.g. Walther et al. 2001, 2002, Doney et al. 2012), the latter process, known as ocean acidification (OA), has only recently been identified as a global concern. Since the Industrial Revolution, increasing atmospheric CO₂ concentrations have raised CO₂ concentrations in the surface of the open ocean and decreased seawater pH by approximately 0.1 units, with an expected further drop of 0.2 to 0.3 units by 2100 (RCP8.5; Hoegh-Guldberg et al. 2014). Furthermore, coastal systems experience an array of acidic sources that the open ocean does not, such as terrestrial and freshwater runoff, coastal upwelling, and changes to watershed dynamics (Duarte et al. 2013), which can increase carbonate system variability and create conditions more acidic than future open ocean projections (e.g. Reum et al. 2014, Wallace et al. 2014). Studies in both open ocean and coastal ecosystems link behavioural impacts in various marine taxa to OA (Munday et al. 2009, Briffa et al. 2012).

Until recently, few studies have addressed potential impacts of OA on marine animal behaviour. Most OA studies have focused primarily on physiology (e.g. Pörtner et al. 2004, Pörtner 2008), calcification (e.g. Ries et al. 2009), and fitness and survivorship (e.g. Kurihara 2008) of larval and juvenile animals. However, increasing evidence shows that OA can influence the behaviour of many marine organisms (Briffa et al. 2012). The recent increase in studies on OA and marine animal behaviour (see Fig. 1) war-

rants a new review to synthesize current knowledge, highlight knowledge gaps, and elucidate areas of research that deserve particular focus. Here we provide a comprehensive overview of the current scientific literature surrounding the impact of OA on marine animal behaviour. We also present a quantitative synthesis, calculating the direction and magnitude of behavioural changes from current conditions under various OA scenarios. Finally, we provide suggestions for future research and highlight key questions requiring attention.

LITERATURE SEARCH AND QUANTITATIVE SYNTHESIS: METHODOLOGY

Literature search and data collection

We conducted an online search for papers through ISI Web of Science and Google Scholar using the keywords 'ocean acidification' or 'acidification' or 'carbon dioxide' or 'CO₂', combined with 'behaviour/behavior' or 'animal behaviour/behavior' within the text of the article. We then limited the search to original research articles that included some measure of behaviour in their analyses. We then carefully checked the reference list of each paper obtained in the online search to find any papers the online literature search may have missed. Both search methods were conducted bi-weekly from September 2014 to June 2015 to ensure that new publications were not missed. The combination of these methods provided extensive coverage of the published literature assessing the effects of OA on marine animal behaviour, yielding a total of 69 papers (Fig. 1).

Data extracted from each paper included general bibliographical information, species studied, life-stage tested, *p*CO₂ levels employed (pH or saturation state (Ω) for studies not reporting *p*CO₂), behaviour(s) or proxy of behaviour(s) measured (i.e. behavioural endpoint(s)), and the absolute % change in a behavioural endpoint from control (see 'Quantitative synthesis' below). In comparison to ambient conditions, we also determined the overall behavioural effect of each OA level, as either positive (a statistically significant increase in a measured behaviour under elevated CO₂), negative (a statistically significant decrease in a measured behaviour under elevated CO₂), no effect (no statistically discernable change in a measured behaviour under elevated CO₂) or a mixed effect (effects in a measured behaviour under elevated CO₂ differing between elevated CO₂ levels). Importantly, we applied these definitions to the

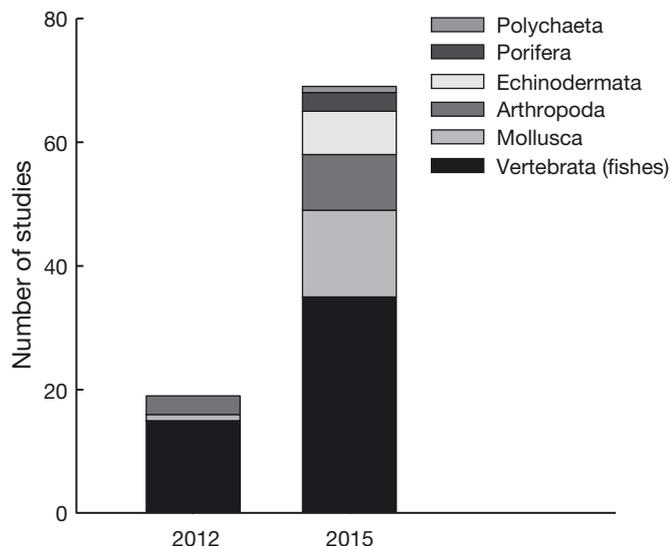


Fig. 1. Total number of studies assessing the impacts of ocean acidification on marine animal behaviour reported in Briffa et al. (2012) ($n = 19$; only included fishes, molluscs, and arthropods) and in this review (2015) ($n = 69$)

overall directionality of the effect and they do not reflect the functional outcome of the behavioural change. For example, we considered increased clownfish activity under elevated CO_2 to be a positive effect, although increased activity could theoretically decrease survival (a negative functional effect).

Quantitative synthesis

We manually extracted raw data from a subset of applicable publications (defined as peer-reviewed publications comparing a directly-measured behavioural endpoint under elevated CO_2 conditions to ambient conditions) obtained from our literature search and calculated the absolute % change in behaviour (defined as the overall % change in behaviour without incorporating directionality of change) from ambient conditions for each OA scenario tested in each publication. Absolute % change was calculated as:

$$\frac{\text{Elevated endpoint} - \text{ambient endpoint}}{\text{Ambient endpoint}} \times 100\%$$

where 'elevated endpoint' is the average measured behaviour under a given OA scenario and 'ambient endpoint' is the average measured behaviour under present-day (i.e. experimental control; 2009–2015) conditions.

To encompass all potential OA scenarios, data include magnitudes for behaviour measured under OA

conditions in isolation, in the context of other environmental parameters, in the context of pH variability, and under a variety of experimental time frames (e.g. some studies examined behaviour in the same CO_2 treatments at different time periods; our analysis included all time periods). However, for the purposes of the quantitative synthesis, we excluded experimental treatments that used a neurotransmitter agonist or antagonist in order to explore GABA_A receptor functioning (see 'The role of GABA ') as a mechanism for a particular behavioural change under OA conditions. Furthermore, for assessing the impacts of transgenerational acclimation and adaptation, we only compared treatments that reared parents and offspring under the same CO_2 conditions. That is, only OA parent-OA offspring treatments were compared to ambient parent-ambient offspring treatments, given that parents and offspring most likely experience similar CO_2 levels at a given time. Finally, the quantitative synthesis included only studies that compared a behavioural endpoint across various acidification groups (e.g. ANOVA-type designs; regressions were excluded) and, as such, does not incorporate every study from our literature review.

Our approach has limitations. For example, values visually estimated from published figures may include some error. Additionally, positive changes can mathematically exceed 100% while negative changes cannot, adding further complication. Despite these limitations, however, the data provide valuable information on the overall magnitude of change, which is important in determining the degree to which future oceanic CO_2 conditions will impact particular organisms.

IMPACTS OF OCEAN ACIDIFICATION ON MARINE ANIMAL BEHAVIOUR

Our literature review indicated that OA influences the behaviour of both vertebrates and invertebrates in multiple ways (Tables 1 & 2). Experimental conditions in the vast majority of published studies employed ambient (control) and CO_2 -enriched (experimental) seawater treatments based on mid- (2050) and end-of-century (2100) OA projections, with the exception of a few studies employing conditions well beyond near-future (i.e. beyond 2100) projections (Tables 1 & 2). Studies typically rear animals in such conditions for a given period of time and then expose them to applicable experiments to measure differences in behaviour between animals from the different rearing conditions. Other studies reared animals

Table 1. Summary of the impacts of elevated CO₂ on marine fish behaviour. Studies are organized chronologically within Teleostei and Elasmobranchii. Effects are reported for experimental treatments looking at the impacts of CO₂ in isolation. ^FStudies that employed field experiments and ^Mstudies that incorporated multiple environmental factors (see Table 4 for alternative effects of multiple factors). L/D: light/dark

Reference	Species	Life stage	Behaviour	pCO ₂	Effect
Teleostei					
Melzner et al. (2009)	<i>Gadus morhua</i>	Juvenile	Swimming	5792 ppm 3080 ppm	None None
Munday et al. (2009)	<i>Amphiprion percula</i>	Larvae	Olfactory discrimination	1050 ppm 1710 ppm	Negative Negative
			Homing	1050 ppm 1710 ppm	Negative Negative
Dixson et al. (2010)	<i>Amphiprion percula</i>	Hatched	Predator detection	1000 ppm	None
		Settling	Predator detection	1000 ppm	Negative
Munday et al. (2010) ^F	<i>Amphiprion percula</i>	Settling	Predator response	550 ppm 700 ppm	None Negative
	<i>Pomacentrus wardi</i>	Settling	Predator response	850 ppm 550 ppm 700 ppm	Negative None Negative
Cripps et al. (2011)	<i>Pseudochromis fuscus</i>	Adult	Olfactory preference	600 µatm 950 µatm	Negative Negative
			Activity	600 µatm 950 µatm	None Positive
			Feeding	600 µatm 950 µatm	Negative None
Ferrari et al. (2011a) ^F	<i>Pomacentrus chrysurus</i>	Juvenile	Predator response	700 ppm 850 ppm	Negative Negative
	<i>P. moluccensis</i>	Juvenile	Predator response	700 ppm 850 ppm	Negative Negative
	<i>P. amboiensis</i>	Juvenile	Predator response	700 ppm 850 ppm	Negative Negative
	<i>P. nagasakiensis</i>	Juvenile	Predator response	700 ppm 850 ppm	Negative Negative
Ferrari et al. (2011b)	<i>Pseudochromis fuscus</i>	Adult	Predation rate (small prey)	700 µatm	None
			Predation rate (large prey)	700 µatm	None
			Prey selectivity (small prey)	700 µatm	None
			Prey selectivity (large prey)	700 µatm	Negative
Simpson et al. (2011)	<i>Amphiprion percula</i>	Juvenile	Auditory predator avoidance	600 µatm 700 µatm 900 µatm	Negative Negative Negative
Devine et al. (2012a) ^F	<i>Cheliodipterus quinquelineatus</i>	Adult	Homing ability	550 ppm 700 ppm 950 ppm	Negative Negative Negative
Devine et al. (2012b)	<i>Pomacentrus chrysurus</i>	Settling	Habitat preference	700 ppm 850 ppm	None Negative
			Settlement rate	700 ppm 850 ppm	None None
	<i>P. moluccensis</i>	Settling	Habitat preference	700 ppm 850 ppm	Negative Negative
			Settlement rate	700 ppm 850 ppm	None Negative
	<i>P. amboiensis</i>	Settling	Habitat preference	700 ppm 850 ppm	None None
			Settlement rate	700 ppm 850 ppm	Negative None
Ferrari et al. (2012a)	<i>Pomacentrus amboiensis</i>	Juvenile	Visual risk assessment	550 µatm 700 µatm 850 µatm	None None Negative
Ferrari et al. (2012b)	<i>Pomacentrus amboiensis</i>	Pre-settling	Predator response	850 µatm	Negative
			Learning	700 µatm	Negative
Domenici et al. (2012)	<i>Neopomacentrus azysron</i>	Settling	Lateralization	880 µatm	Negative
Nilsson et al. (2012)	<i>Amphiprion percula</i>	Larvae	Olfactory presence	900 µatm	Negative
	<i>Neopomacentrus azysron</i>	Settling	Lateralization	900 µatm	Negative

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Table 1 (continued)

Reference	Species	Life stage	Behaviour	pCO ₂	Effect
Nowicki et al. (2012) ^M	<i>Amphiprion melanopus</i>	Juvenile	Food consumption	530 µatm	None
			Activity	960 µatm	None
Allan et al. (2013)	<i>Pseudochromis fuscus</i>	Adult	Predation success	530 µatm	None
			Predation rate	960 µatm	None
			Attack distance	880 µatm	None
	<i>Pomacentrus amboiensis</i>	Juvenile	Reaction distance	880 µatm	None
			Looming threshold	880 µatm	None
Devine & Munday (2013) ^F	<i>Paragobiodon xanthosomus</i>	Adult	Escape distance	880 µatm	Negative
	<i>Gobiodon histrio</i>	Adult	Habitat preference	880 µatm	Negative
Jutfelt et al. (2013)	<i>Gasterosteus aculeatus</i>	Adult	Habitat preference	880 µatm	Negative
			Boldness	990 µatm	Negative
			Exploration	990 µatm	Negative
			Lateralization	990 µatm	Negative
Hamilton et al. (2014)	<i>Sebastes diplora</i>	Juvenile	Learning	990 µatm	Negative
	<i>Gadus morhua</i>	Larvae	L/D preference (anxiety)	1125 µatm	Negative
Maneja et al. (2013)	<i>Gadus morhua</i>	Larvae	Swimming	1400 µatm	None
				4200 µatm	None
McCormick et al. (2013)	<i>Pomacentrus moluccensis</i>	Settling	Activity	945 µatm	None
			Aggressiveness	945 µatm	Positive
			Aggressiveness	945 µatm	Positive
Munday et al. (2013)	<i>Plectopomus leopardus</i>	Juvenile	Activity	945 µatm	Negative
				570 µatm	None
				700 µatm	Negative
				960 µatm	Negative
Allan et al. (2014)	<i>Amphiprion melanopus</i>	Juvenile	Predator avoidance (hiding)	570 µatm	None
				700 µatm	Negative
Chivers et al. (2014)	<i>Pomacentrus amboiensis</i>	Juvenile	Activity	987 µatm	Negative
			Feeding	987 µatm	Negative
			Learning	987 µatm	Negative
			Lateralization	987 µatm	Negative
Domenici et al. (2014) ^M	<i>Pomacentrus wardi</i>	Juvenile	Lateralization	921 µatm	Negative
	<i>Pseudochromis fuscus</i>	Adult	Predation rate	995 µatm	None
Ferrari et al. (2015) ^M	<i>Pseudochromis fuscus</i>	Adult	Prey selectivity	995 µatm	Negative
				995 µatm	Negative
Munday et al. (2014)	<i>Dascyllus aruanus</i>	Juvenile	Olfactory discrimination	441–998 µatm	Negative
			Predator avoidance	441–998 µatm	Negative
			Activity	441–998 µatm	Negative
			Boldness	441–998 µatm	Positive
				441–998 µatm	Positive
	<i>Pomacentrus moluccensis</i>	Juvenile	Olfactory discrimination	441–998 µatm	Negative
			Predator avoidance	441–998 µatm	Negative
			Activity	441–998 µatm	Negative
			Boldness	441–998 µatm	Positive
				441–998 µatm	Positive
	<i>Apogon cyanosoma</i>	Juvenile	Olfactory discrimination	441–998 µatm	Negative
			Predator avoidance	441–998 µatm	Negative
			Activity	441–998 µatm	Positive
			Boldness	441–998 µatm	Positive
				441–998 µatm	Positive
<i>Chelodipterus quinquelineatus</i>	Juvenile	Olfactory discrimination	441–998 µatm	Negative	
		Predator avoidance	441–998 µatm	Negative	
		Activity	441–998 µatm	Positive	
		Boldness	441–998 µatm	Positive	
			441–998 µatm	Positive	
Welch et al. (2014)	<i>Acanthochromis polyacanthus</i>	Juvenile	Predator avoidance	656 µatm	Negative
				912 µatm	Negative
			Lateralization	656 µatm	None
				912 µatm	Negative
			Olfactory prey tracking	741 µatm	None
				1064 µatm	Negative
Jutfelt & Hedgärde (2015)	<i>Gadus morhua</i>	Juvenile	Boldness	1000 µatm	None
			Lateralization	1000 µatm	None
				1000 µatm	None
Lai et al. (2015)	<i>Gasterosteus aculeatus</i>	Adult	Lateralization	992 µatm	Negative
Näslund et al. (2015)	<i>Gasterosteus aculeatus</i>	Adult	Predator avoidance	1000 µatm	None
			Lateralization	1000 µatm	Negative

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Table 1 (continued)

Reference	Species	Life stage	Behaviour	$p\text{CO}_2$	Effect
Sundin & Jutfelt (2015)	<i>Ctenolabrus rupestris</i>	Juvenile	Predator avoidance	995 μatm	Negative
			Lateralization	995 μatm	None
			Activity	995 μatm	None
Elasmobranchii					
Dixson et al. (2014)	<i>Mustelis canis</i>	Adult	Activity	741 μatm	None
				1064 μatm	None
			Attacking prey	741 μatm	Negative
				1064 μatm	Negative
Green & Jutfelt (2014)	<i>Scyliorhinus canicula</i>	Adult	Swimming	900 μatm	Negative
			Lateralization	900 μatm	Negative
Heinrich et al. (2015)	<i>Hemiscyllium ocellatum</i>	Adult	Foraging behaviour	615 μatm	None
				910 μatm	None

in ambient CO_2 water and simply introduced them to experimentally acidified environments. As such, all of the studies assessing the impacts of OA on marine animal behaviour were experimental in nature. Although most employed laboratory experiments, some studies (7 out of 69) employed field experiments by rearing animals in the laboratory under elevated CO_2 conditions and then introducing them to a natural environment (i.e. current, ambient conditions); with the exception of Green et al. (2009, 2013), who manipulated sediment pH and aragonite saturation with crushed shell hash in the field and quantified natural clam settlement, and Munday et al. (2014), who collected fishes from sites naturally mimicking present-day and near-future (2100) CO_2 conditions and used them in laboratory-based behavioural experiments (Tables 1 & 2).

Our quantitative analysis found an average change of 233 and 41% in behavioural endpoints (i.e. the measured behaviour in a given experiment) for vertebrates and invertebrates, respectively, between present-day conditions and end-of-century projections. The smaller set of studies that tested CO_2 conditions projected for 2050 and 2300 found a mean change in vertebrate behaviour between present day and 2050 and present day and 2300 of 21 and 4% (likely reflective of low sample size), respectively, in contrast to a mean 84% change in invertebrate behaviour between present day and 2300. However, the direction (positive, negative, no effect) and magnitude (% change in behaviour from ambient conditions) of these impacts varied considerably (Table 3, Fig. 2), with apparently greater impact on vertebrates (Fig. 2). The following sections synthesize the current literature outlining the influence of OA on the behaviour of vertebrate and invertebrate marine taxa in detail.

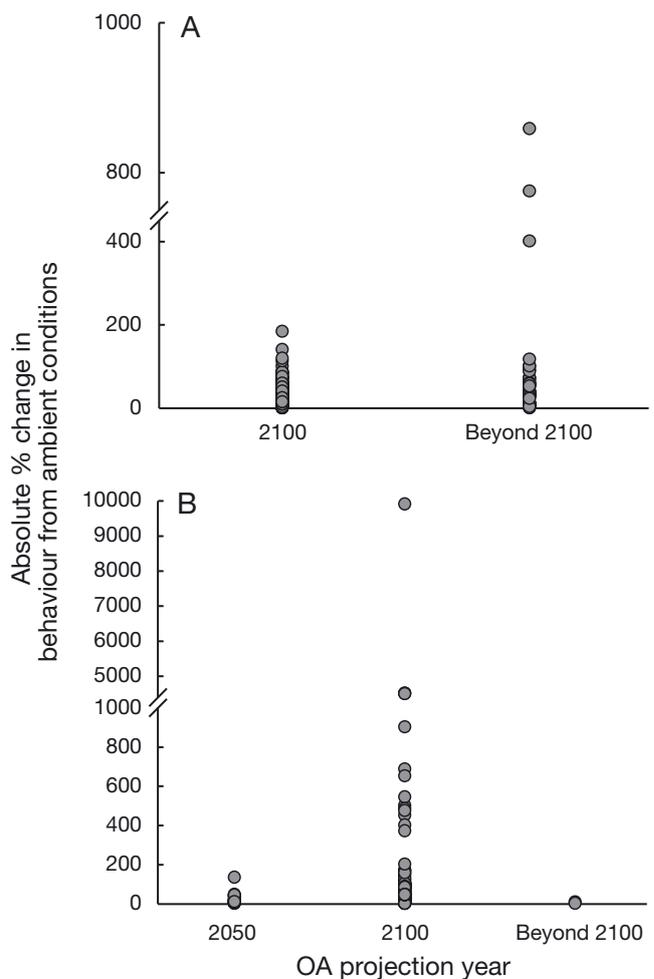


Fig. 2. Scatterplot depicting reported impact magnitudes (absolute % change in all endpoints from ambient conditions) of ocean acidification (OA) on (A) marine invertebrate and (B) vertebrate behaviour for mid-century (2050), end-of-century (2100), and beyond end-of-century OA scenarios. Absolute % change is the overall % change in behaviour without incorporating directionality of change

Table 2. Summary of the impacts of elevated CO₂ on marine invertebrate behaviour. Taxonomic groups are ordered according to phylogenetic chronology and studies are organized chronologically within their respective phylum. Effects are reported for treatments assessing CO₂ in isolation. ^FStudies that employed field experiments and ^Mstudies incorporating multiple environmental factors (see Table 4 for alternative effects of multiple factors). Ω: carbonate (aragonite) saturation state

Reference	Species	Life stage	Behaviour	pCO ₂	Effect
Porifera					
Albright et al. (2010)	<i>Acropora palmata</i>	Larvae	Settlement	~650 µatm ~880 µatm	Negative Negative
Doropoulos et al. (2012)	<i>Acropora millepora</i>	Larvae	Settlement	807 µatm 1299 µatm	Negative Negative
Webster et al. (2013)	<i>Hydrolithon onkodes</i>	Larvae	Settlement	822 µatm 1187 µatm 1638 µatm	Negative Negative Negative
Annelida					
Widdicombe & Needham (2007)	<i>Nereis virens</i>	Adult	Burrowing	Not reported pH: 7.3 pH: 6.5 pH: 5.6	None None None
Mollusca					
Bibby et al. (2007)	<i>Littorina littorea</i>	Adult	Predator avoidance	Not reported pH: 6.63	Positive
Ellis et al. (2009)	<i>Littorina obtusata</i>	Embryonic	Spinning time Spinning rate Crawling Periodization	1093 ppm 1093 ppm 1093 ppm 1093 ppm	None Negative Negative Negative
Green et al. (2009) ^F	<i>Mya arenaria</i>	Settling	Settlement	Not reported pH: 7.32	Negative
Schalkhausser et al. (2013)	<i>Pecten maximus</i>	Adult	Clapping amount Clapping force	1135 µatm 1135 µatm	None Negative
Green et al. (2013) ^F	<i>Mercenaria mercenaria</i>	Plantigrade	Burrowing	Not reported Ω: 0.68 Ω: 0.05–1.05	Negative Negative
Manríquez et al. (2013)	<i>Concholepas concholepas</i>	Juvenile	Self-righting	716 µatm 1036 µatm	Positive Positive
Vargas et al. (2013)	<i>Concholepas concholepas</i>	Larvae	Feeding Food selectivity	700 ppm 1000 ppm 700 ppm 1000 ppm	Negative Negative Negative Negative
Watson et al. (2014)	<i>Gibberulus gibberulus gibbosus</i>	Adult (jumping) Adult (non-jumping)	Predator escape Predator escape	961 µatm 961 µatm	Negative Positive
Clements & Hunt (2014)	<i>Mya arenaria</i>	Juvenile	Burrowing Dispersal	Not reported Ω: 0.05–1.05 Not reported Ω: 0.05–1.05	Negative Positive
Manríquez et al. (2014)	<i>Concholepas concholepas</i>	Larvae Juveniles	Prey detection Predator response Prey detection Predator response	700 µatm 1000 µatm 700 µatm 1000 µatm 700 µatm 1000 µatm	None None None Negative None None
Sanford et al. (2014)	<i>Urosalpinx cinerea</i>	Juvenile	Drilling predation	1000 µatm	Negative
Spady et al. (2014)	<i>Idiosepius pygmaeus</i>	Not reported	Activity	1000 µatm 626 µatm 956 µatm	None Positive Positive
Vargas et al. (2014)	<i>Concholepas concholepas</i>	Larvae	Feeding rate	700 µatm 1000 µatm	Negative Negative
	<i>Perumytilus purpuratus</i>	Juvenile	Feeding	700 µatm 1000 µatm	Negative Negative

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Table 2 (continued)

Reference	Species	Life stage	Behaviour	pCO ₂	Effect
Queirós et al. (2015) ^M	<i>Nucella lapillus</i>	Adults	Activity (speed)	750 ppm	Negative
				1000 ppm	Negative
			Foraging time	750 ppm	None
				1000ppm	None
			Foraging distance	750 ppm	None
				1000 ppm	Negative
			Prey handling time	750 ppm	None
				1000 ppm	Negative
Arthropoda					
de la Haye et al. (2011)	<i>Pagurus bernhardous</i>	Adult	Shell detection	12191 µatm	No effect
			Shell selection	12191 µatm	Negative
			Antennular flicking	12191 µatm	Negative
			Movement	12191 µatm	Negative
Dissanayake & Ishimatsu (2011) ^M	<i>Metapenaeus joyneri</i>	Adult	Swimming	11054 µatm	Negative
Alenius & Munguia (2012)	<i>Paradella diana</i>	Adult	Activity	Not reported	
				pH 7.60 stable	None
				pH 7.60 variable	Negative
Appelhans et al. (2012)	<i>Carcinus maenas</i>	Adult	Feeding	1120 µatm	No effect
				4000 µatm	Negative
de la Haye et al. (2012)	<i>Pagurus bernhardous</i>	Adult	Foraging	12061 µatm	Negative
			Movement	12061 µatm	Negative
			Antennular flicking	12061 µatm	Negative
Li & Gao (2012)	<i>Centropages tenuiremis</i>	Planktonic	Sensitivity	1000 µatm	None
				>1700 µatm	Negative
				1000 µatm	Positive
Landes & Zimmer (2012) ^M	<i>Carcinus maenas</i>	Small adult	Feeding rates		
			Prey handling time	377–539 µatm	None
		Large adult	Prey selectivity	377–539 µatm	None
			Prey handling time	377–539 µatm	Negative
			Prey selectivity	377–539 µatm	None
Saba et al. (2012)	<i>Euphausia superba</i>	Adult	Feeding rate	672 ppm	Negative
Zittier et al. (2013) ^M	<i>Hyas araneus</i>	Adult	Self-righting	750 µatm	Positive
				1120 µatm	Positive
				3000 µatm	Positive
Echinodermata					
Chan et al. (2011)	<i>Dendraster excentricus</i>	Larvae	Swimming	1000 ppm	None
Appelhans et al. (2012)	<i>Asterias rubens</i>	Adult	Feeding	1250 µatm	None
				3500 µatm	Negative
Burnell et al. (2013) ^M	<i>Amblypneustes pallidus</i>	Juvenile	Grazing	640 µatm	Positive
Uthicke et al. (2013)	<i>Acanthaster planci</i>	Larvae	Settlement	877 µatm	Negative
Appelhans et al. (2014)	<i>Asterias rubens</i>	Juvenile	Feeding	1120 µatm	Negative
				4000 µatm	Negative
			Self-righting	1120 µatm	None
				4000 µatm	None
Barry et al. (2014) ^F	<i>Strongylocentrotus fragilis</i>	Adult	Movement	3255 ppm	None
			Foraging	3255 ppm	Negative
Chan et al. (2015)	<i>Strongylocentrotus droebachiensis</i>	Larvae	Swimming	Not reported	
				pH: 7.3	None
				pH: 6.5	None

Vertebrates

Although studies have assessed teleost and elasmobranch fishes, the vast majority have focused on teleost coral reef fishes (Fig. 3, Table 1). Despite the narrow range of vertebrate taxa assessed, studies suggest a wide array of OA effects on marine fish behaviour (Table 3).

Laboratory studies clearly define the effects of elevated CO₂ conditions on the predator–prey interactions of fishes, particularly in coral reefs (Fig. 3). Dixon et al. (2010) reported that, in contrast to fish raised under ambient CO₂ conditions, settlement-stage clownfish larvae (*Amphiprion percula*; 11 d post-hatching) raised under elevated CO₂ conditions could not distinguish predator olfactory cues from

Table 3. The relative number of behaviours (as displayed in Tables 1 & 2; each label under the column 'behaviour' was treated as a single data point) exhibiting a positive effect, negative effect, no effect, or mixed effect (any combination of the previous 3; dependent upon different CO₂ levels tested) to ocean acidification for vertebrates and invertebrates

	Positive	Negative	No effect	Mixed	Total
Vertebrates					
Teleostei	8	47	23	13	91
Reef fishes	8	42	21	13	84
Other	0	5	2	0	7
Elasmobranchii	0	3	2	0	5
Total	8	49	26	13	96
Invertebrates					
Mollusca	5	13	6	4	28
Arthropoda	2	9	5	2	18
Echinodermata	1	3	4	1	9
Porifera	0	3	0	0	3
Polychaeta	0	0	1	0	1
Total	8	28	16	7	59

those of non-predators and spent more time in the presence of other fish cues regardless of species; however, no such behavioural shift occurred under elevated CO₂ in newly hatched larvae. Similarly, Munday et al. (2010) reported negative impacts on predator avoidance responses (time spent in water containing a predator cue) in settlement-stage clownfish (*A. percula*) and damselfish (*Pomacentrus wardi*), and these negative behavioural impacts directly affected field survival of laboratory-reared *P. wardi*. Munday et al. (2014) also reported reduced predator avoidance in 2 damselfish and 2 cardinalfish species residing in coral reefs with naturally elevated CO₂ (CO₂ seeps) in comparison to fishes residing in ambient CO₂ reefs. Attraction to predators (rather than avoidance) under elevated CO₂ was also reported in coral trout *Plectropomus leopardus* (Munday et al. 2013) and goldsinny wrasse *Ctenolabrus rupestris*

(Sundin & Jutfelt 2015). Conversely, OA had no effect on avoidance of seabird predation (as measured by sheltering response) by marine 3-spined stickleback *Gasterosteus aculeatus* (Näslund et al. 2015).

Other responses of fish prey to predators may also be hindered under elevated CO₂ conditions (Table 1). For example, Ferrari et al. (2012a) reported reduced intensity of response to visual predator cues in juvenile damselfish (*Pomacentrus amboinensis*) under elevated CO₂, while 30 to 95% decreases in antipredator responses were reported for 4 species of juvenile damselfishes (Ferrari et al. 2011a). Also, while juvenile clownfish (*A. percula*) reared under ambient CO₂ conditions avoided audio recordings of predator-rich reef conditions, those reared in elevated CO₂ conditions did not, suggesting that OA can diminish auditory response in reef fishes (Simpson et al. 2011). Rearing under elevated CO₂ hindered escape behaviour (the time to locate an exit point and successfully exit an enclosure) of the 3-spined stickleback *G. aculeatus* (Jutfelt et al. 2013), and also reduced responses (apparent looming, reaction, and escape distances) of damselfish to predatory, ambient-CO₂ dottybacks (*Pseudochromis fuscus*) (although the effect diminished when predators also raised under elevated CO₂) (Allan et al. 2013).

Cognitive functioning in marine fishes can also be impacted by OA. Chivers et al. (2014) and Ferrari et al. (2012b) both reported that juvenile damselfish (*P. amboinensis*) reared under elevated CO₂ were unable to learn the identity of their predators and consequently suffered reduced behavioural defences. Likewise, Jutfelt et al. (2013) reported diminished learning of escape behaviours in the 3-spined stickleback *G. aculeatus* reared under high CO₂. Impaired behavioural lateralization—the preference for moving right or left—has also been reported in coral reef fishes (*Neopomacentrus azysron*; Domenici et al. 2012; *P. wardi*; Domenici et al. 2014) and a temperate

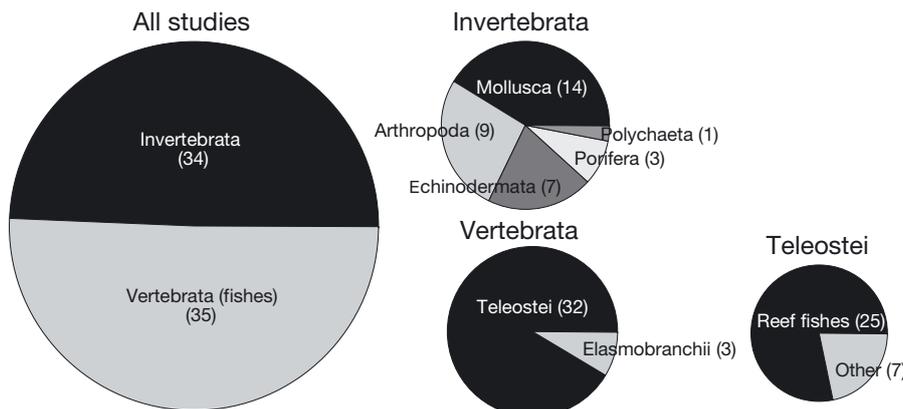


Fig. 3. Studies that have assessed the impact of ocean acidification on the behaviour of marine animals distributed according to taxon. Pie slice areas depict the relative percentages of the corresponding taxonomic group. Values in parentheses indicate the total number of publications incorporating the corresponding taxonomic group into the study (n = 69). Totals of lower taxonomic levels do not necessarily add to those of higher levels due to the incorporation of >1 taxonomic group in some studies

fish (*G. aculeatus*: Jutfelt et al. 2013, Lai et al. 2015, Näslund et al. 2015). Conversely, juvenile Atlantic cod *Gadus morhua* (Jutfelt & Hedgärde 2015) and goldsinny wrasse *C. rupestris* (Sundin & Jutfelt 2015) appear unaffected by OA, and the small-spotted catshark *Scyliorhinus canicula* exhibited increased lateralization under elevated CO₂ (Green & Jutfelt 2014), suggesting differences in OA-induced behavioural responses between taxonomic groups and/or ecosystems. Transgenerational acclimation, in which the parental environmental experience influences the offspring's 'normal' reaction under similar conditions, may not alleviate OA effects on behavioural lateralization in coral reef fishes (Welch et al. 2014), but increased temperature may (Domenici et al. 2014).

Reduced antipredator responses in marine fishes can lead to increased predation under elevated CO₂ conditions. For example, dottyback (*Pseudochromis fuscus*) predation on several species of damselfishes increased under elevated CO₂ due to hindered damselfish escape responses (Ferrari et al. 2011b). However, predatory behaviour can also be negatively impacted by elevated CO₂. Cripps et al. (2011) reported increased activity and reduced attraction to prey odour in elevated CO₂-reared dottybacks (*P. fuscus*), while Dixon et al. (2014) found decreased attraction to prey odour in predatory dogfish (*Mustelus canis*). Conversely, juvenile wrasse (*C. rupestris*) activity (Sundin & Jutfelt 2015), and epaulette shark *Hemiscyllium ocellatum* foraging (Heinrich et al. 2015) appear unaffected by elevated CO₂. Nowicki et al. (2012) reported increased feeding rates of juvenile anemonefish (*Amphiprion melanopus*) under elevated CO₂ and temperature, but no significant effects of OA at present-day temperatures. Furthermore, while Ferrari et al. (2011b) reported increased predation rates and reduced prey selectivity in brown dottyback (*P. fuscus*) reared under elevated CO₂, Ferrari et al. (2015) demonstrated that elevated temperatures reversed the effects of increased CO₂ on prey selectivity and amplified predation rates, resulting in abnormally high predation rates.

Various other aspects of fish behaviour can be altered by elevated CO₂. Under elevated CO₂, Jutfelt et al. (2013) reported increased shyness in the 3-spined stickleback *G. aculeatus* and Hamilton et al. (2014) reported increased anxiety (i.e. more time spent in dark) in Californian rockfish (*Sebastes diploproa*), the latter resulting from hindered GABA_A receptor functioning. Conversely, 4 species of damselfishes exhibited increased boldness in the presence of predator cues under elevated CO₂ (Ferrari et al. 2011a). Munday et al. (2014) observed increased

boldness but contrasting effects on activity levels for damselfishes and cardinalfishes exposed to naturally elevated CO₂. Similarly, McCormick et al. (2013) reported increased activity in *P. amboinensis* and decreased activity in *Pomacentrus moluccensis* under elevated CO₂, which reversed the relative aggressiveness and habitat-specific competitive dominance of these 2 species.

Elevated CO₂ can also affect homing ability and settlement in marine fishes. When raised under elevated CO₂ conditions, adult cardinalfish (*Cheilodipterus quinquelineatus*) could not distinguish between home- and foreign-site odours (Devine et al. 2012a). Similarly, clownfish (*A. percula*) larvae reared under elevated CO₂ conditions were more attracted to settlement stimuli that ambient-reared larvae avoided and, unlike ambient-reared larvae, were unable to distinguish their parents from other conspecific adults (Munday et al. 2009). Devine et al. (2012b) reported that the larvae of 2 damselfishes (*P. amboinensis* and *P. moluccensis*) lost the acute ability to discriminate between the odours of 3 habitat types (hard-bottom, soft-bottom, or coral rubble), while *P. chrysurus* was unaffected by elevated CO₂; however, within 24 h, all 3 species were able to settle in their preferred habitat, possibly by using secondary settlement cues (e.g. visual) under OA conditions. Similarly, Devine & Munday (2013) reported that the coral gobies *Paragobiodon xanthosomus* and *Gobiodon histrio* were unable to identify and choose their habitat (the coral *Seriatopora hystrix*) when reared under elevated CO₂.

Near-future (2100) OA has been reported to impact fish swimming behaviour, albeit only in a single species. Swimming duration in the small-spotted catshark *S. canicula* was longer in elevated CO₂-reared sharks (Green & Jutfelt 2014). In contrast, juvenile and larval Atlantic cod *G. morhua* swimming is highly resilient to OA, as swimming speed, duration, distance, turn angles, and resting time are reportedly unaffected by elevated CO₂ levels far beyond those projected for 2100 (Melzner et al. 2009, Maneja et al. 2013, Jutfelt & Hedgärde 2015).

Invertebrates

Compared to vertebrates, OA effects on invertebrate behaviour have been explored in a wider variety of taxa (Fig. 3, Table 2). Similarly, however, studies suggest a range of negative, positive, and absence of OA effects on marine invertebrate behaviour (Table 3).

Molluscs

Like coral reef fishes, predator–prey interactions among molluscs are likely to be influenced by OA, although reported effects vary across species. Watson et al. (2014) reported hindered conch snail (*Gibberulus gibberulus gibbosus*) predator avoidance resulting from GABA_A receptor interference, with the number of snails jumping, the number of jumps per snail, and the jumping distance in the presence of a predator reduced under elevated CO₂. In contrast, Queirós et al. (2015) demonstrated that dog whelk *Nucella lapillus* foraging distance and time increased under more acidic conditions, likely enhancing feeding but potentially increasing susceptibility to predators. While some measures of king scallop *Pecten maximus* escape performance (i.e. clapping force) were negatively affected by elevated CO₂, others (i.e. number of claps) were not (Schalkhausser et al. 2013). Manríquez et al. (2014) reported that predator (crab, *Acanthocyclus hassleri*) avoidance by larval and newly-settled muricid snails (*Concholepas concholepas*) was negatively impacted by elevated CO₂, but the ability of both stages of *C. concholepas* to detect prey (mussels, *Perumytilus purpuratus*) was undiminished. Spady et al. (2014) observed that pygmy squid (*Idiosepius pygmaeus*) switched modes of defense under elevated CO₂, but reported no effects on frequency of defense. Sanford et al. (2014) found that the total number of oysters (*Ostrea lurida*) drilled by invasive predatory gastropods (*Urosalpinx cinerea*) increased when oysters were reared under elevated CO₂, regardless of predator CO₂ rearing conditions. Elevated CO₂ has also been reported to induce positive effects on predator avoidance in juvenile *C. concholepas*, as self-righting (ability to reattach foot to substrate following dislodgement) increased under elevated CO₂ (Manríquez et al. 2013). Although conditions were well beyond those of near-future (2100) OA projections, Bibby et al. (2007) reported increased predator (*Carcinus maenas*) avoidance behaviour in intertidal gastropods (*Littorina littorea*) under elevated CO₂, which they attributed to reduced physiological defences (shell thickness and oxygen consumption). Feeding behaviour and efficiency in gastropods (*C. concholepas*) (Vargas et al. 2013, 2014) and bivalves (*Perumytilus purpuratus*) (Vargas et al. 2013) feeding on plankton has also been reported to decrease under elevated CO₂.

Elevated CO₂ can also influence the movement and activity of marine molluscs. Ellis et al. (2009) found that intertidal gastropod (*Littorina obtusata*) embryos raised under elevated CO₂ spent more time station-

ary and less time swimming and crawling compared to ambient CO₂-reared embryos. Further, the spinning rate of embryonic snails was lower and periodization—the average length of time that the embryos spent between periods of movement and non-movement—was greater in elevated CO₂ embryos than those reared in ambient CO₂ (Ellis et al. 2009). Similarly, movement speed in adult *N. lapillus* decreased under elevated CO₂, while foraging time was unaffected, and foraging distance and prey handling time increased; warming negated the OA effects on speed and foraging distance (Queirós et al. 2015). In contrast, activity and movement of pygmy squid (*I. pygmaeus*) increased under both moderate and severe near-future (2100) projections of elevated CO₂ (Spady et al. 2014).

In addition to water column acidification, sediment porewater acidification can influence the behaviour of infaunal molluscs. Green et al. (2013) reported that settling hard clams *Mercenaria mercenaria* rejected and did not burrow into more acidic sediments, while Green et al. (2009) reported negative effects of more acidified sediment on soft-shell clam *Mya arenaria* settlement. Clements & Hunt (2014) observed similar results for burrowing of juvenile *M. arenaria* and also observed that the subsequent dispersal of juvenile clams was increased in more acidified sediments. Although both studies used sediment geochemical conditions beyond near future surface ocean projections, conditions fell within the range currently observed in surface-sediment porewater along the northwest Atlantic coast. Furthermore, while the behavioural responses to sediment acidification have been attributed to lower carbonate saturation state within bottom sediments, the specific biological mechanism(s) underpinning bivalve burrowing and dispersal responses to sediment acidification remain unknown.

Arthropods

Marine arthropods are reported to experience a variety of OA behavioural effects. For example, Disanayake & Ishimatsu (2011) reported decreased swimming speed in prawns (*Metapenaeus joyneri*) reared under pH conditions far beyond those projected for 2100 (pH 6.8), although elevated temperature attenuated the impacts of low pH. Although stable low pH conditions did not alter the swimming speed or time spent swimming, crawling, conglobating (curling into a ball), or resting of intertidal isopods (*Paradella diana*) subjected to predator

harassment, variable low pH conditions decreased swimming speed, swimming time, and crawling time (Alenius & Munguia 2012).

Feeding rates of Antarctic krill *Euphausia superba* were higher under elevated CO₂ conditions; however, metabolic activity and nutrient excretion also increased, suggesting that negative shifts in physiological processes could result in reduced growth and reproduction despite positive shifts in feeding behaviour (Saba et al. 2012). Conversely, feeding and clearance rates of copepods (*Centropages tenuiremis*) declined after 24 h of elevated CO₂ exposure, but increased dramatically after 36 and 90 h (Li & Gao 2012). Appelhans et al. (2012) reported that green crab *Carcinus maenas* feeding rates were reduced by a 10 wk exposure to pH conditions beyond those expected by 2100 (pH 7.38), but not by those expected for 2100 (pH 7.8). In contrast, Landes & Zimmer (2012) reported that OA did not alter the *C. maenas* and *L. littorea* predator–prey interaction, although individual physiological effects were observed for each species. Foraging behaviour (time spent in contact with a food cue, time spent moving, and antennular flicking rate) in hermit crabs (*Pagurus bernhardus*) was also reduced under CO₂ conditions beyond those predicted for 2100 (CO₂ ~12000 ppm, pH 6.8) (de la Haye et al. 2012).

For predator escape behaviours, Zittier et al. (2013) reported that the righting response of adult spider crabs (*Hyas araneus*) was unaffected by elevated CO₂ alone, but reduced when both CO₂ and temperature were elevated, suggesting that spider crabs may be more vulnerable to predators in a warm, high CO₂ ocean. In addition, de la Haye et al. (2011) reported that assessment and choice behaviour (time required to change shells, movement time, and antennular flicking) of hermit crabs (*P. bernhardus*) was negatively impacted under elevated CO₂ conditions beyond end-of-century projections.

Echinoderms

The impacts of OA on echinoderm behaviour are less studied than in molluscs and arthropods. Elevated CO₂ conditions (slightly higher than end-of-century projections) increased sea urchin (*Amblypneustes pallidus*) grazing, although this effect was offset by increased eutrophication (Burnell et al. 2013). Barry et al. (2014) found that foraging time of a deep-sea urchin, *Strongylocentrotus fragilis*, was increased under elevated CO₂ conditions, but foraging speed was unaffected. Although not directly

measured, the feeding performance of larval sand dollars (*Dendraster excentricus*) has been suggested to decline under elevated CO₂, as the stomachs and bodies of sand dollars reared in elevated CO₂ were smaller than ambient CO₂-reared conspecifics (Chan et al. 2011). Appelhans et al. (2012, 2014) also reported that prey consumption in sea stars (*Asterias rubens*) feeding on bivalves (*Mytilus edulis*) was lower in sea stars exposed to elevated CO₂, although sea star righting response was not impacted.

For swimming performance and settling behaviours, Chan et al. (2011) reported that larval sand dollar (*D. excentricus*) feeding performance was negatively impacted by OA, but elevated CO₂ did not affect the speed, trajectory, or direction of larval swimming. Likewise, Chan et al. (2015) observed that decreased pH had no impact on the swimming behaviour of larval green sea urchins *Strongylocentrotus droebachiensis*. In contrast, Uthicke et al. (2013) reported that settlement success of larval sea stars *Acanthaster planci* on crustose coralline algal (CCA) was lower in sea stars exposed to elevated CO₂, but only when the CCA substrate was also exposed to elevated CO₂ for 85 d.

Other taxa

Other invertebrates known to experience behavioural changes in response to OA include corals and polychaete worms (Widdicombe & Needham 2007, Albright et al. 2010, Doropoulos et al. 2012, Webster et al. 2013) (Table 2). The settling behaviour, metamorphosis, and recruitment of coral larvae decreases under elevated CO₂, a likely consequence of altered interactions between corals and their symbiotic zooxanthellae (Albright et al. 2010, Doropoulos et al. 2012, Webster et al. 2013). The burrowing activity of *Nereis virens* (Polychaeta) was unaffected in more acidified sediments (Widdicombe & Needham 2007). Given the severe lack of research addressing the behavioural impacts of elevated CO₂ on these and other understudied invertebrate taxa, a comprehensive understanding of how OA will impact the behaviour of these animals is not yet possible and more research involving such taxonomic groups is warranted. Although molluscs, arthropods, and echinoderms are among the more diverse and abundant invertebrates, understanding OA effects on behaviours of lesser-studied animals is necessary to fully understand how their populations and associated communities and ecosystems may be impacted by OA.

THE ROLE OF GABA

Studies have suggested GABA_A receptor disruption to be a mechanism by which behaviour is impaired by OA (Nilsson et al. 2012, Chivers et al. 2014, Hamilton et al. 2014, Watson et al. 2014, Lai et al. 2015). GABA (gamma-aminobutyric acid) is an inhibitory neurotransmitter found in the central and peripheral nervous systems of vertebrates and in the peripheral nervous system of some invertebrates (Jessen et al. 1979), which opens ion channels and promotes the flow of ions in and out of cells (Nilsson et al. 2012). There are 2 receptors

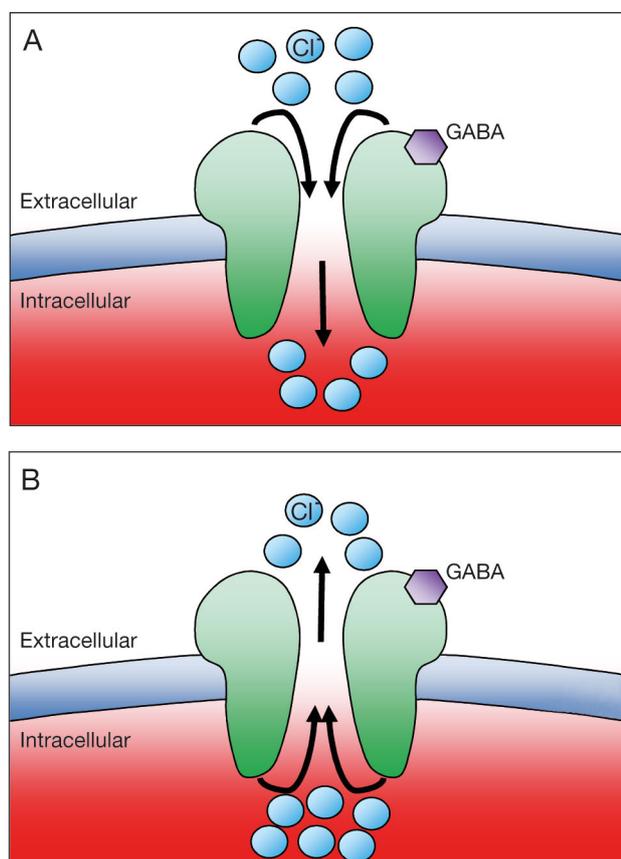


Fig. 4. Visual representation of GABA_A-receptor functioning via ion gradients under (A) ambient (present-day) and (B) elevated CO₂ conditions. Under ambient conditions, extracellular [Cl⁻] and [HCO₃⁻] (only [Cl⁻] depicted; [HCO₃⁻] not shown) is slightly higher than intracellular [Cl⁻] and [HCO₃⁻], maintaining the equilibrium potential near the resting membrane potential. Under elevated CO₂, acidosis is counteracted through the excretion of Cl⁻ and the accumulation of HCO₃⁻, altering the ion gradient across the neural membrane and potentially resulting in membrane depolarization, neural pathway excitation, and altered behaviour. GABA_A receptor functioning may be potentiated or reversed, depending on the magnitude of Cl⁻ and HCO₃⁻ changes in acid-base regulation. Adapted from Hamilton et al. (2014)

associated with GABA: GABA_A and GABA_B. Of these, the GABA_A receptor is of particular concern with OA because of its specific conductance for Cl⁻ and HCO₃⁻—the 2 ions most likely to be impacted by OA. Mechanistically, under ambient CO₂ conditions, extracellular Cl⁻ and HCO₃⁻ concentrations are slightly higher than intracellular concentrations, maintaining the equilibrium potential near resting membrane potential (Nilsson et al. 2012). When GABA_A receptors open, Cl⁻ and HCO₃⁻ flow into the cell, preventing depolarization, maintaining a negative membrane potential, and reducing neural activity (Nilsson et al. 2012). However, under elevated CO₂, animals excrete Cl⁻ and accumulate HCO₃⁻ from the external environment (i.e. seawater) to prevent acidosis (e.g. Heuer & Grosell 2014). This alters the ion gradient across the neural membrane and can potentially result in membrane depolarization, neural pathway excitation, and altered behaviour (Fig. 4).

Since the GABA_A receptor is particularly vulnerable to OA, studies have focused on elucidating this pathway as a mechanism for behavioural changes under elevated CO₂. For example, treating fishes exposed to elevated CO₂ with gabazine—a GABA_A antagonist—can alleviate negative behavioural effects of OA (Nilsson et al. 2012, Hamilton et al. 2014, Chivers et al. 2014, Lai et al. 2015). Similar results have also been reported for a marine gastropod (*Gibberulus gibberulus gibbosus*) (Watson et al. 2014), although more work is needed pertaining to GABA_A's role in invertebrate behaviour under elevated CO₂. Given that GABA is more predominant in vertebrates than invertebrates and that vertebrates heavily rely on GABA for motor and sensory function, the influence of OA on GABA_A may explain why fishes appear more susceptible to the behavioural effects of OA than invertebrates. However, this explanation may not fully explain all behavioural changes associated with OA. Other physiological functions (see Table 1 in Briffa et al. 2012) can act independently or synergistically with GABA_A to alleviate or amplify OA effects on some behaviours (e.g. swimming behaviour or predator escape). For example, although predator escape behaviour in coral reef fishes under elevated CO₂ can be hindered via GABA_A interference, physical changes to structures involved in sensory functions, such as otoliths (e.g. Bignami et al. 2013), may act to amplify or negate negative behavioural changes. Such physiological changes in response to OA can be variable among species (e.g. Munday et al. 2011) and warrant more research.

Although thought to be important in marine animal behaviour (both vertebrates and invertebrates), the role of GABA in decision making for many animals, particularly invertebrates, is still poorly understood. For example, GABA receptors are found in the pedal ganglia of bivalves (e.g. Vitellaro-Zuccarello & De Biasi 1988, Karhunen et al. 1993, Welsh et al. 2014) and GABA has been suggested to increase settlement in some bivalve species (García-Lavandeira et al. 2005, Mesías-Gansbiller et al. 2008), although other neurotransmitters, most notably epinephrine, are also involved in bivalve settlement (García-Lavandeira et al. 2005, Mesías-Gansbiller et al. 2008). Although it is plausible that GABA_A interference could be responsible for bivalve burrowing responses and is likely to be responsible in other cephalized (nervous tissue concentrated toward one end—head—of the animal) invertebrates, the specific mechanism(s) involved in bivalve burrowing behaviour are not well defined and studies definitively elucidating this mechanism in bivalves and other invertebrate taxa are needed.

Ultimately the behavioural effects of OA are likely to be driven by a variety of changes (positive or negative) that may act synergistically or independently to alter behaviour. Studies should thus work toward an understanding of how multiple OA effects act to change animal behaviour and relate such findings to other important ecological endpoints (e.g. survival, ecosystem functioning, biodiversity). Furthermore, a better understanding of the link between acid-base regulation and GABA_A receptor functioning under elevated CO₂ may explain species specific effects and provide a holistic understanding of OA effects on marine animal behaviour.

INTERACTIVE EFFECTS OF MULTIPLE ENVIRONMENTAL PARAMETERS

Multiple environmental drivers (e.g. temperature, salinity, eutrophication) can act synergistically, antagonistically, or independently of OA to impact various biological processes (e.g. Denman et al. 2011, Bopp et al. 2013). For example, increasing temperature can attenuate, amplify, or have no impact on the direction and magnitude of biological changes observed under elevated CO₂ alone (Table 4). As such, understanding how other environmental drivers may interact with elevated CO₂ is critical to understanding how OA will impact animal behaviour.

Although studies have started to assess how other environmental drivers may interact with OA to yield

biological effects, knowledge is limited. With respect to animal behaviour, only 8 studies have assessed OA in the context of other drivers, suggesting contrasting outcomes for different species and behaviours (Table 4). With the exception of a single study (Burnell et al. 2013), only temperature–CO₂ interactions have been assessed (Table 4), resulting in different effects than those imposed by OA alone. Nowicki et al. (2012) reported that, under elevated CO₂ and temperature, anemonefish (*Amphiprion melanopus*) food consumption increased, whereas elevated CO₂ alone had no effect. Conversely, Domenici et al. (2014) reported that negative impacts of OA on behavioural lateralization in *Pomacentrus wardi* were attenuated under higher temperatures. Ferrari et al. (2015) found that higher temperatures amplified negative effects of elevated CO₂ on dottyback (*Pseudochromis fuscus*) predation rates, but acted antagonistically to attenuate the negative impact of OA on prey selectivity. Similarly to OA alone, elevated temperature and OA had no effect on the predator–prey interaction between *Carcinus maenas* and *Littorina littorea* (Landes & Zimmer 2012). Increased temperature attenuated the OA effect on prawn (*Metapenaeus joyneri*) swimming behaviour (Dissanayake & Ishimatsu 2011) and negatively impacted activity capacity in spider crabs (*Hyas araneus*) (Zittier et al. 2013). Increased temperature also amplified the OA effect on sea urchin grazing capacity (*Amblypneustes pallidus*), although this was partially attenuated under eutrophic conditions (Burnell et al. 2013).

It is clear that OA effects on marine animal behaviour will be influenced by co-occurring environmental changes. The complex interactions between multiple environmental drivers highlight the importance of assessing OA in synergy with other factors. Although elevated temperature appears to predominantly alleviate the impacts of elevated CO₂ (Table 4), studies should focus on understanding how OA will impact behaviour in association with other co-occurring environmental changes, including hypoxia, salinity, and eutrophication.

HIGH CO₂ BEHAVIOUR IN THE CONTEXT OF ENVIRONMENTAL VARIABILITY

When assessing the impacts of OA on marine species, biological responses are typically measured under relatively stable carbonate system conditions mimicking end-of-century projections. Although this may be reasonable for the buffered open

Table 4. Summary of studies assessing the impacts of OA on marine animal behaviour in the context of co-occurring environmental parameters

Species	Additional factor(s)	Behaviour	Acidification	Observed effect Acidification + additional factor(s)	Reference
Vertebrates					
<i>Amphiprion melanopus</i>	Elevated temperature (31.5°C)	Foraging	No effect	Synergistic positive effect of elevated temperature and pCO ₂ (963 µatm); negative effect of elevated temperature at ambient and moderate pCO ₂ (419 and 529 µatm, respectively)	Nowicki et al. (2012)
<i>Pomacentrus wardi</i>	Elevated temperature (31°C)	Behavioural lateralization	Negative	Increased temperature attenuated impacts of elevated pCO ₂ (935 µatm)	Domenici et al. (2014)
<i>Pomacentrus amboinensis</i> and <i>P. nagasakiensis</i>	Elevated temperature (31°C)	Predation	No effect	Synergistic positive effect of elevated temperature and pCO ₂ (1006.7 µatm)	Ferrari et al. (2015)
		Prey selectivity	No effect	Synergistic negative effect of elevated temperature and pCO ₂ (1006.7 µatm)	
Invertebrates					
<i>Metapenaeus joyneri</i>	Elevated temperature (25°C)	Swimming	Negative	Increased temperature attenuated impacts of elevated pCO ₂ (11053.5 µatm)	Dissanayake & Ishimatsu (2011) ^a
<i>Carcinus maenas</i>	Elevated temperature (8–18°C)	Prey handling time	No effect	No effect	Landes & Zimmer (2012)
<i>Hyas araneus</i>	Elevated temperature (4–12°C)	Activity capacity	No effect	Synergistic negative effect of elevated temperature and 3 degrees of elevated pCO ₂ (750, 1120, and 3000 µatm)	Zittler et al. (2013)
<i>Amblypneustes pollidus</i>	Elevated temperature (20°C) and eutrophication (enriched nutrients)	Grazing	Positive	Synergistic positive effect of elevated temperature and pCO ₂ (650.9 µatm); enriched nutrients partially attenuated this synergistic effect, though not completely	Burnell et al. (2013)
<i>Nucella lapillus</i>	Elevated temperature (2°C above ambient; ambient not provided)	Activity	Negative	Increased temperature attenuated impacts of elevated pCO ₂ (750 ppm)	Queirós et al. (2015)
		Foraging	Negative	Increased temperature attenuated impacts of elevated pCO ₂ (750 ppm)	

^aOnly tested acidification conditions beyond near-future predictions

ocean, present-day oceanic CO₂ concentrations are known to vary spatially and temporally, particularly in coastal regions (e.g. Duarte et al. 2013, Waldbusser & Salisbury 2014), driven by a variety of biotic and abiotic factors (e.g. Hinga 2002, Blackford & Gilbert 2007, Doney et al. 2007, Dore et al. 2009). However, the ways in which carbonate system variability will respond to a changing climate are still unknown (e.g. Helmuth et al. 2014). Given the highly complex spatial and temporal variability in the marine carbonate system and the uncertainty of how climatic variability will respond to changing conditions, it is imperative that studies assess the behavioural impacts of carbonate system variability on marine species. Since such variability can modulate an organism's duration of exposure to conditions above, at, or below those that may elicit a biological effect, as well as increase or decrease the frequency and magnitude of extremes that an organism experiences (e.g. Shaw et al. 2013), variability can offset or amplify OA effects on behaviour. For example, Alenius & Munguia (2012) found stable low pH conditions (7.60 ± 0.01 (SE); approx. range 7.5–7.7) had no impact on isopod (*Paradella diana*) swimming behaviour and harassment response, but increased variability around the low pH mean (7.60 ± 0.03 (SE); approx. range 7.3–8.0) had a negative impact on both behaviours.

Because OA effects on behaviour have primarily been determined under relatively stable CO₂ conditions, it is unclear how well results will allow us to predict effects in more variable coastal systems. Although the reported results for larval reef fishes are likely accurate since they reside in the well-buffered open ocean, coastal species are likely to experience more variable conditions (Duarte et al. 2013, Waldbusser & Salisbury 2014). Because we cannot yet predict environmental variability in the future, it is difficult to apply such parameters accurately to experimental designs (e.g. Helmuth et al. 2014). As a result, research programs should be developed to predict carbonate system variability under projected future means to accurately determine the behavioural effects of coastal OA. Moreover, carbonate system variability should be coupled with variability in other environmental drivers. Although difficult and highly complex, such studies would provide much more predictive power for understanding OA effects on behaviour and would advance understanding toward a much-needed unifying theory for large scale predications regarding the biological impacts of OA.

ACCLIMATION AND ADAPTATION POTENTIAL

While most studies assessing OA effects on behaviour employ only one life history stage, some have addressed the potential for transgenerational and temporal acclimation and adaptation to alleviate single-generation effects. While the negative effects of OA on the escape performance of juvenile reef fish were partially alleviated by parental exposure to elevated CO₂ (Allan et al. 2014), transgenerational acclimation and adaptation had no impact on the negative effects of OA on predator avoidance and lateralization in juvenile damselfish (*Acanthochromis polyacanthus*; Welch et al. 2014). Appelhans et al. (2014) reported that juvenile sea star (*Asterias rubens*) feeding behaviour and righting response did not display acclimation potential over a 6 wk period. Similar effects in the laboratory and field for fishes residing in naturally elevated CO₂ environments also suggest that temporal acclimation and adaptation are insufficient to offset OA effects on reef fish behaviour (Munday et al. 2014).

Populations can also adapt to OA through genetic adaptation, where the offspring of successfully reproducing individuals in an OA-exposed population inherit successful traits from parents to tolerate elevated CO₂ (Shaw & Etkerson 2012). Although genetic adaptation has been tested for physiological endpoints (e.g. Schlegel et al. 2012, 2015), the role of genetic heritability in alleviating OA effects on behaviour remains untested. However, approaches to such experiments have been proposed (Sunday et al. 2014) and provide a template for expanding OA-behaviour research into this realm. Ultimately, at present, acclimation and adaptation do not appear sufficient in reducing OA effects on behaviour, but more research is certainly warranted.

GENERALIZATIONS AND FUTURE RESEARCH

Ocean acidification is likely to impact marine animal behaviour in a myriad of ways. While invertebrates appear more vulnerable to OA physiologically, fishes appear to be more affected behaviourally, with the direction and magnitude of OA effects likely to vary across species, ecosystems, and behaviours. Not all studies have used realistic OA scenarios and behavioural responses appear unpredictable beyond pCO₂ conditions of ~1000 µatm; however, such studies should not be considered in the context of near-future (2050–2100) OA. Furthermore, behavioural changes do not always result in negative outcomes,

but can elicit positive and/or negative impacts. For example, the overall outcome of bivalves rejecting more acidic sediments can positively reduce 'death by dissolution' (Green et al. 2009, 2013, Clements & Hunt 2014), but increase vulnerability to other mortality factors (Hunt & Scheibling 1997). As such, more research exploring an array of species, systems, and behaviours is necessary to understand how OA affects behaviour and how this translates to populations, communities, and ecosystems. The interactive effects of multiple environmental drivers and their associated variability require immediate attention, along with the potential of transgenerational acclimation and adaptation, to diminish the effects of OA in subsequent generations. Additionally, a mechanistic understanding of the link between acid-base regulation and GABA_A receptor functioning under elevated CO₂ could potentially resolve species-specific responses. Detailed suggestions for future OA-behaviour research for vertebrates and invertebrates are given below.

Vertebrates

Predator-prey interactions, homing ability, choice and discriminatory behaviour, auditory response, learning, foraging, exploratory behaviour, and behavioural lateralization in marine fishes have all been reported to be affected by OA, while other behaviours, such as swimming behaviour, appear relatively unaffected. Although the impacts of OA on marine fishes are well documented, studies have predominantly focused on coral reef fishes. Given the specialized nature of coral reef ecosystems and the high degree of biodiversity in comparison to most other systems, it is important to expand OA-fish behaviour studies to more taxa residing outside of coral reefs. Furthermore, among the studies that have been conducted, contrasting results for fish species within coral reef systems suggest that OA effects on fish behaviour are species specific. It is thus necessary to better understand the mechanistic association between acid-base regulation and GABA_A receptor functioning, as this could reconcile species-specific effects and lead to an overarching theory of how OA affects behaviour. Although co-occurring environmental drivers (e.g. temperature, salinity, oxygen, eutrophication) will interact with OA to alleviate or amplify the effects of elevated CO₂ on marine fish behaviour, studies incorporating multiple drivers are limited (Table 2). Furthermore, environmental variability is neglected in OA-fish behaviour studies.

As such, research is needed to determine how changes in multiple environmental drivers will interact with OA to impact marine fish behaviour and how variability associated with these drivers will influence behaviour in coastal fish species. Finally, although some studies have marked and observed laboratory-reared fish in the wild (e.g. Ferrari et al. 2011a, Devine et al. 2012a), most studies rely on laboratory experiments. More field studies of fish behaviour in areas of naturally elevated CO₂ should be conducted to broaden the current understanding of how OA will or potentially already has impacted the behaviour of marine fishes.

Invertebrates

Although OA will impact the behaviour of marine invertebrates, the impacts will likely be variable across species, ecosystems, and behaviours. For example, the direction and magnitude of OA effects on predator-prey relationships will depend on the dynamics of the system and species involved, with different behaviours being impacted in different ways. OA effects on invertebrate behaviour may differ across developmental stages for an individual species as well. Given the contrasting results within and between species and systems, coupled with the lack of OA-induced behavioural research for some groups of organisms (e.g. corals, polychaetes, and a myriad of other invertebrate taxa), research employing different systems and taxonomic groups is warranted. Although GABA_A receptor interference seems to be a widely applicable mechanism for OA impacts on vertebrate behaviour, our mechanistic understanding of OA effects on invertebrate behaviour is rudimentary and requires more research. As with fishes, understanding the link between acid-base regulation and GABA_A receptor functioning could account for observed species specificity and help to develop a unifying theory of OA effects on invertebrate behaviour.

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