

# Eating in an acidifying ocean: a quantitative review of elevated CO<sub>2</sub> effects on the feeding rates of calcifying marine invertebrates

Jeff C. Clements  · Elizabeth S. Darrow

Received: 12 March 2018 / Revised: 18 May 2018 / Accepted: 22 May 2018 / Published online: 1 June 2018  
© Crown 2018

**Abstract** Feeding is fundamental for all heterotrophic organisms, providing the means to acquire energy for basic life processes. Recent studies have suggested that experimental ocean acidification (OA) can alter the feeding performance of marine calcifying invertebrates, but results have been inconsistent. While several reviews pertaining to the biological effects of OA exist, none provide a synthesis of OA effects on feeding performance. Here, we provide a quantitative analysis of published experiments testing for effects of elevated CO<sub>2</sub> on feeding rates of marine calcifying invertebrates. Results revealed that suspension-feeding molluscs and predatory and grazing echinoderms experienced depressed feeding rates

under elevated CO<sub>2</sub>, while arthropods appeared unaffected; larval and juvenile animals were more susceptible to CO<sub>2</sub> effects than adults. Feeding strategy did not appear to influence the overall taxonomic trend, nor did habitat, although exposure time did have an effect. AIC model selection revealed that Phylum best predicted effect size; life stage and exposure time were also included in candidate models. Based on these results, we synthesize potential physiological attributes of different taxa that may drive OA sensitivities in feeding rates, which could potentially result in community-level impacts. We also discuss CO<sub>2</sub> effects on calcifier feeding in the context of elevated temperature and other global marine change stressors, and highlight other areas for future research.

---

Handling editor: Iacopo Bertocci

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10750-018-3665-1>) contains supplementary material, which is available to authorized users.

---

J. C. Clements (✉)  
Aquaculture and Coastal Ecosystems Section, Fisheries and Oceans Canada, Gulf Fisheries Centre, 343 Université Avenue, Moncton, NB E1C 9B6, Canada  
e-mail: jefferyclements@gmail.com

E. S. Darrow  
Department of Biology and Marine Biology, Center for Marine Science, University of North Carolina Wilmington, 5600 Marvin K. Moss Lane, Wilmington, NC 28409, USA

**Keywords** Carbon dioxide · pH · Invertebrate · Global change · Physiology

## Introduction

Maintaining energy balance in the face of environmental stressors is fundamental to life. The amount of food an animal consumes, when balanced with energetic losses (due to various functions such as metabolic processes, growth, development, repair, activity, reproduction, homeostatic maintenance, thermal regulation), can dictate the animal's energy

reserves. Since basic biological functions are sustained by available food reserves during periods of depressed food supply (Kooijman, 2009), animals that are unable to gather and process food efficiently may inevitably exhaust these reserves faster than animals that can feed and process food more effectively. An inability to feed effectively may therefore negatively impact the above-mentioned core functions, in turn impacting organism survival (Pepin et al., 2014). Thus, although several other processes are involved, examining animals' feeding responses to stressors is one way to estimate energy acquisition.

Given the important link between feeding and fitness (survival and reproduction), it is important to understand the environmental factors that can influence feeding for marine organisms. These can include (but are not limited to) food availability (Wong & Cheung, 2001), temperature (Sanford, 2002; Norman, 2012), salinity (Lankford Jr. & Targett 1994; Chaparro et al., 2008), and oxygen concentrations (Pihl et al., 1992; Breitburg et al., 1994). In addition, ocean acidification (OA) is recognized as one of the greatest threats to marine biodiversity (Secretariat of the Convention on Biological Diversity, 2009; Hendriks et al., 2010; Howes et al., 2015). OA describes the reduction in oceanic pH and associated alterations to the marine carbonate system resulting from the absorption of excess anthropogenic CO<sub>2</sub> by the oceans (Caldeira & Wickett, 2003; Orr et al., 2005). Since the onset of the Industrial Revolution, surface ocean pH has dropped by ~ 0.1 units and is expected to decline by further 0.2–0.3 units by the end of this century (RCP8.5 scenario; Hoegh-Guldberg et al., 2014). In estuarine and coastal environments where high productivity, terrestrial (nutrient) and freshwater input, and upwelling can lead to large diurnal and seasonal fluctuations in pH, the effects of OA are more variable and can be locally altered (Cai et al., 2011; Duarte et al., 2013). Given the intrinsic link between an organism's physiology and its environment, it is thus important to consider the potential effects of OA on the feeding rates of marine organisms.

While OA is likely to have impacts on many marine organisms (Kroeker et al., 2013), the energetic costs of calcification and reliance on a calcium carbonate shell or skeleton make calcifying taxa some of the most vulnerable to OA effects (Orr et al., 2005; Ries et al., 2009; Hofmann et al., 2010; Howes et al., 2015). Resistant taxa are likely to be those that can offset effects

of adverse water chemistry by maximizing feeding and energy use efficiency. The energetic costs of calcification are generally suggested to increase under elevated *p*CO<sub>2</sub> conditions (but see e.g. Schoepf et al., 2013 for exceptions); however, at present, insufficient empirical evidence exists to successfully decouple the costs of calcium carbonate precipitation from perturbations of homeostatic maintenance, metabolic processes, and acid–base perturbations to the costs of each of these processes independently (Fernández-Rieriz et al., 2011). Recent evidence has suggested that if enough food is available, some marine calcifiers may be able to overcome these energetic constraints and succeed under conditions of elevated *p*CO<sub>2</sub> (Thomsen et al., 2013; Pan et al., 2015; Towle et al., 2015; Ramajo et al., 2016a, b). However, food availability is highly variable in marine systems, and it is unknown how future climate change may impact a populations' food sources. Consequently, species in which feeding rates are depressed under elevated *p*CO<sub>2</sub> are likely to be negatively impacted. In contrast, species exhibiting increased feeding efficiency under elevated *p*CO<sub>2</sub> may be able to tolerate OA. The limits of such physiological tolerances can select “winners” and “losers” on an ecosystem scale under future OA scenarios.

Studies assessing the impact of OA on marine calcifier feeding have been increasing recently. However, while numerous reviews pertaining to the biological effects of OA exist (Gazeau et al., 2013; Harvey et al., 2013; Kroeker et al., 2013; Wittman & Pörtner, 2013; Clements & Hunt, 2015; Lefevre, 2016), none provide a quantitative analysis of OA effects on feeding rates. Here, we provide a quantitative synthesis of OA effects on the feeding rates of calcifying marine invertebrates by reviewing published experiments. We identified groups of marine organisms that may be differentially impacted by OA with respect to their feeding rates, propose mechanisms to explain these differences, and discuss knowledge gaps and prospects for future research.

## Methods

### Literature search and data collection

Articles were searched for via Web of Science and Google Scholar (up until March, 2017) using the keywords ‘ocean acidification’ or ‘carbon dioxide’

plus ‘feeding rate’ and/or ‘ingestion rate’ and/or ‘consumption rate’ and/or ‘clearance rate’ anywhere in article (all raw data in Table S1). We then conducted a cited literature search of each article obtained from the online literature search to collect any articles that may have been missed in the online search. This provided us with a reasonable number of publications to test hypotheses regarding OA effects on calcifier feeding rates ( $n = 55$ ; see *Results*). While studies exist testing effects of OA-exposed food (i.e. active prey or passive food particles) on feeding of consumer organisms reared under ambient conditions (e.g. Amaral et al., 2012; Rossoll et al., 2012; Dupont et al., 2015; Benítez et al., 2016; Duarte et al., 2016; Isari et al., 2016), we only included studies that reared the target consumer organism under elevated  $p\text{CO}_2$  to describe the direct effects of OA on feeding. Consumer organisms were either predators, grazers, or suspension feeders. For data comparability, feeding rates, grazing rates, ingestion rates, clearance rates, and filtration rates were included as comparable measures of feeding.

To control for local adaptation, we assumed that each study chose control  $p\text{CO}_2$  conditions appropriate for their target species. The highest pH level (or lowest  $p\text{CO}_2$  level) employed in each experiment from each study was considered the control treatment and we considered all  $p\text{CO}_2$  levels  $> 600 \mu\text{atm}$  (low-end prediction for 2050) as OA treatments; intermediate  $p\text{CO}_2$  levels  $< 600 \mu\text{atm}$  were discarded. For studies reporting different acclimation periods or experimental durations, we considered all acclimation times in our analyses. We considered each experimental treatment as an individual data point (as per Harvey et al., 2013; Kroeker et al., 2013). Thus, if studies used  $> 1$  experimental assay, species, size, relevant  $p\text{CO}_2$  level, or food supply, we treated each as an individual observation. For experiments that tested the combined effects of acidification and other environmental stressors (i.e. warming and hypoxia) on feeding rates, we only assessed differences between acidification groups for the control/ambient levels of the other factors.

From each study, we collected general information for each species tested, including Phylum, life history stage (larval, juvenile, or adult), feeding strategy at the life stage assessed (suspension, grazer, deposit, predator, or scavenger), and whether the life stage tested was a benthic or pelagic consumer. We also collected general study information, including units used to

measure feeding performance, geographic location from which the animals were collected, pH and/or  $p\text{CO}_2$  conditions of each relevant OA treatment, and duration that individuals were reared under experimental or control conditions prior to feeding measurements (hereafter referred to as ‘acclimation duration’, measured in days). Each of these parameters was then divided into categories (Table 1). Acclimation duration categories were chosen to represent a range of exposure times (see Table 1). The  $p\text{CO}_2$  categories were based on upper-end projections for various time periods, including before year 2100 (i.e. end-of-century;  $< 1000 \mu\text{atm}$ ), 2100–2200 (1000–1500  $\mu\text{atm}$ ), 2200–2300 (1501–2000  $\mu\text{atm}$ ), and beyond 2300 ( $> 2000 \mu\text{atm}$ ); it is important to note that these categories all fall within the range of currently observed  $p\text{CO}_2$  values in many nearshore coastal systems.

### Effect size analysis

To determine individual and mean effect sizes, we recorded the mean feeding rate, variance (standardized as standard deviation), and sample size for each OA treatment and control treatment for each observation in each study. These values were obtained from published tables, were digitally estimated from published graphs using Image J or PlotDigitizer, were obtained from online databases, or directly from corresponding authors. Means, variances, and sample sizes were used to calculate natural log response ratios (effect size, LnRR) for each experimental group. LnRR is the ratio of the experimental effect to the control effect (natural log transformed). An LnRR value of 0 signifies no effect of the experimental treatment on the response variable, while negative and positive LnRR values signify negative and positive effects, respectively (Hedges et al., 1999). We used LnRR as an effect size because this metric has a high capacity to detect true effects and is robust to low sample sizes (Lajeunesse & Forbes, 2003).

Weighted random effects models were used to derive mean effect sizes (LnRR) for each level in each of the 6 a priori factors outlined in Table 1; mean effect sizes were only calculated for taxa and/or life history stages containing 3 or more observations ( $n \geq 3$ ; corals were excluded from the effect size analysis for failing to meet this criterion [ $n = 2$ ]). Bootstrapped (10,000 replicates) bias corrected and

**Table 1** A priori factors and their respective levels and sample sizes (number of studies and number of experimental treatments) derived to assess OA effects on marine calcifier feeding rates in this study

Factor	Levels	<i>n</i> (studies)	<i>n</i> (treatments)
Phylum	Mollusca	23	94
	Arthropoda	21	70
	Echinodermata	10	23
	Porifera	2	2
Feeding strategy	Suspension	20	87
	Grazer	16	54
	Predator	19	48
<i>p</i> CO <sub>2</sub> level	< 1000 μatm	21	37
	1000–1500 μatm	32	80
	1501–2000 μatm	8	13
	> 2000 μatm	20	48
Acclimation duration	1–5 days	13	33
	6–10 days	7	19
	11–20 days	8	20
	21–60 days	14	31
	61–100 days	13	61
	> 100 days	5	17
Habitat	Benthic	37	100
	Pelagic	19	89
Life history stage	Larvae	9	41
	Juvenile	18	60
	Adult	29	88

The factors and levels were used for both the statistical outcome analysis and the effect size analysis. Sample sizes do not necessarily add up to 55 (for studies) or 189 (for treatments), as studies may have incorporated > 1 level, or may have neglected to report the level, of a given factor

accelerated (BCa) 95% confidence intervals were used to determine statistical significance (significance occurs when 95% confidence interval does not cross 0). *Q* tests ( $\alpha \leq 0.05$ ) were used to test for heterogeneity in effect sizes among studies. All analyses were conducted using R v. 3.3.0 (R Development Core Team, 2016); effect size calculations and analyses were conducted using the Metafor package (Viechtbauer, 2010).

#### Identifying predictors of calcifier feeding responses to elevated CO<sub>2</sub>

Once effect sizes were derived for all experimental observations, we used model selection to determine which variables (Phylum, Feeding Strategy, Habitat, Life Stage, Acclimation Time, and *p*CO<sub>2</sub>) best predicted effect size. Because “experiment” was used as our unit of replication, we built additive linear mixed effects models (using the “nlme” package in R; Pinheiro et al., 2017) for all possible combinations of predictor variables with “experiment” included as a random variable; we also included a null model (i.e.

model without any fixed predictor variables; random factor of “experiment” only). Prior to model construction, we determined the correlation between each of the predictor variables—if two variables had a correlation  $\geq 0.80$ , then any models incorporating those factors together were discarded (see Table S2). This resulted in a total of 59 models. We then used Akaike’s Information Criterion (AIC; using the “AICcmodavg” package in R [Mazerolle, 2017]) to determine which predictor variables contributed most to explaining effect size variance (Burnham & Anderson, 2002; Anderson, 2007). Models were selected based on AIC and log likelihood values, whereby best models are indicated by the lowest AIC and highest log likelihood values (Burnham & Anderson, 2002). We considered all models with a delta AIC ( $\Delta$  AIC)  $\leq 2$  as top candidate models, as those with a  $\Delta$  AIC  $\leq 2$  cannot be confidently identified as inadequate models and thus eliminated (Burnham & Anderson, 2002). All analyses were conducted using R v. 3.3.0 (R Development Core Team, 2016).

## Results

### Literature search

Our literature search revealed a total of 55 studies assessing the effects of OA on feeding rates in marine calcifying invertebrates, published between 2008 and March, 2017 (Table 2) and spanning across 46 different geographic locations (Fig. 1). Most studies occurred in Europe ( $n = 20$ ), North America ( $n = 10$ ), Asia ( $n = 10$ ), Australia ( $n = 7$ ), and South America ( $n = 5$ ) ( $N_{\text{location}} = 53$  due to the lack of location information from one study [Houlbrèque et al., 2015] and the utilization of pre-existing data in another study [Jager et al., 2016]). Studies from the eastern coast of South America and the whole of Africa were completely absent, as well as from Greenland, northern Canada and Alaska, central America, western Australia, and northeastern Asia; there was a single study from Antarctica (Fig. 1).

There was a substantial increase in OA-invertebrate feeding rate studies over the past 3 years (2014–2016; Fig. 1). Most studies assessed the effect of OA on feeding rates in molluscs and arthropods (41 and 38%, respectively), with fewer studies focusing on echinoderms (18%) and corals (4.0%). With respect to mode of feeding, studies equally focused on suspension feeders, grazers, and predators (34.5, 34.5, and 30.9%, respectively). Based on our literature review, no studies have tested the effects of OA on feeding rates in deposit feeders or scavengers (although Zhang et al. (2015) assessed energy absorption in a benthic scavenging mollusc, *Nassarius conoidalis* (Deshayes, 1832)). Studies have focused more on benthic (67.3%) than pelagic (34.5%) organisms and have put more of an emphasis on adults (50.9%) and juveniles (36.4%) compared to larvae (16.4%) (life stage percentages total > 100% because one study tested both larval and juvenile individuals; Vargas et al., 2015). Across all studies, control  $p\text{CO}_2$  conditions ranged from 191 to 963  $\mu\text{atm}$ , while elevated  $p\text{CO}_2$  conditions spanned from 593 to 9274  $\mu\text{atm}$ . Control  $p\text{CO}_2$  ranged from 191 to 963, 325 to 871, and 380 to 654 for molluscs, arthropods, and echinoderms, respectively (respective means = 457, 519, and 469). Elevated  $p\text{CO}_2$  conditions were similarly broad for molluscs and echinoderms, while the two coral studies employed a narrower range of  $p\text{CO}_2$  conditions and the arthropods encompassed a far broader range; the

average elevated  $p\text{CO}_2$  treatment was similar across taxa (Fig. 2). Experiments testing for effects on adult and juvenile calcifier feeding encompassed a similarly broad range of  $p\text{CO}_2$  conditions, while the range was narrower for larval experiments (Fig. 2). Within studies, the magnitude of difference between control and elevated  $p\text{CO}_2$  was typically less than 1000  $\mu\text{atm}$ , which is in line with near-future projections.

Of the 55 studies identified in our literature search, 21 (38.2%) assessed OA effects on feeding rates alongside ocean warming (i.e.  $\leq +5^\circ\text{C}$  warming; Table 2). While this sample size is too low to include in a meta-analysis, a comparison of statistical outcomes between OA only treatments and OA + warming treatments in those studies revealed that OA + warming treatments resulted in a far higher percentage of increased feeding rates than of null responses, while the percentage of decreased feeding responses remained about the same (Fig. 3).

### Effect size analysis

$\text{CO}_2$ -induced acidification significantly reduced feeding rates for marine calcifiers (Fig. 4a), but these effects varied by taxon, life history stage, and feeding mechanism. Most  $Q$  tests for heterogeneity of effect sizes within a priori groups were significant, indicating that effect sizes varied significantly among studies (Table S4). The only groups with significant effect tests with non-significant  $Q$  tests were larval echinoderms, pelagic echinoderms, and grazing molluscs, indicating consistent negative effects for these groups across studies.

Feeding rates of molluscs and echinoderms were the most sensitive to elevated  $\text{CO}_2$  (Fig. 4a). With all Phyla pooled, larvae and juveniles showed significantly reduced feeding responses to  $p\text{CO}_2$ , but these responses varied by taxon. All molluscan life stages were negatively affected, but on average, arthropod feeding rates were unaltered across life stages; echinoderm larvae and juveniles showed significantly reduced feeding, but adults did not (Fig. 4b). With all Phyla pooled, only suspension feeders had a significantly negative feeding response to OA; grazers and predators did not (Fig. 4c). Molluscs were the only Phylum occupying the suspension-feeding category; grazing molluscs also had a negative response to elevated  $\text{CO}_2$ . Both predatory and grazing echinoderms displayed significantly reduced feeding rates

**Table 2** Summary of the observed statistical outcomes (increase, decrease, or null effect) and the overall outcome of individual studies testing for OA effects on marine calcifier feeding performance

Phylum	References	Statistical outcome(s)			Overall outcome	Mixed effect driver(s)	
		Increase	Decrease	Null			
Mollusca	Fernández-Rieriz et al. (2011)		●	●	≠	<i>p</i> CO <sub>2</sub> level and animal size	
	Fernández-Reiriz et al. (2012)			●	–		
	Navarro et al. (2013)		●		↓		
	Liu & He (2012)	●	●		≠	Species	
	Burton-Sanders et al. (2013)			●	–		
	Ko et al. (2013)		●	●	≠	<i>p</i> CO <sub>2</sub> level	
	<b>Russell et al. (2013)</b>			●	–		
	Vargas et al. (2013)		●		↓		
	Sanford et al. (2014)	●			↑		
	Vargas et al. (2015)		●	●	≠	<i>p</i> CO <sub>2</sub> level, location, time of measurement	
	<b>Wang et al. (2015)</b>			●	●	≠	Acclimation duration
	<b>Cole et al. (2016)</b>			●		↓	
	<b>Le Moullac et al. (2016)</b>				●	–	
	<b>Navarro et al. (2016)</b>			●		↓	
	<b>Noisette et al. (2016)</b>				●	–	
	Ramajo et al. (2016a, b)	●				↑	
	Stapp et al. (2017)			●	●	≠	<i>p</i> CO <sub>2</sub> level
	Sui et al. (2016)			●	●	≠	Acclimation duration
	Ventura et al. (2016)			●	●	≠	<i>p</i> CO <sub>2</sub> level
	Xu et al. (2016)				●	–	
	<b>Harvey &amp; Moore (2017)</b>			●	●	≠	<i>p</i> CO <sub>2</sub> level
	<b>Tate et al. (2017)</b>				●	–	
	Arthropoda	Watson et al. (2017)		●		↓	
Kurihara et al. (2008)				●	–		
Appelhans et al. (2012)			●	●	≠	<i>p</i> CO <sub>2</sub> level and acclimation duration	
Li & Gao (2012)			●	●	≠	Acclimation duration	
Saba et al. (2012)		●		●	≠	Whether or not the animal was pregnant	
<b>Arnberg et al. (2013)</b>				●	–		
Christmas (2013)			●	●	≠	Species	
<b>Poore et al. (2013)</b>				●	–		
Pedersen et al. (2014)				●	–		
Dodd et al. (2015)			●		↓		
Isari et al. (2015)				●	–		
<b>Li et al. (2015)</b>				●	–		
Thor & Oliva (2015)		●		●	≠	<i>p</i> CO <sub>2</sub> level and acclimation duration	
Campanati et al. (2016)				●	–		
Cooper et al. (2016)			●	●	≠	Acclimation duration	
Cripps et al. (2016)				●	–		
<b>Glandon &amp; Miller (2016)</b>				●	–		



**Table 2** continued

Phylum	References	Statistical outcome(s)			Overall outcome	Mixed effect driver(s)
		Increase	Decrease	Null		
Echinodermata	Hildebrandt et al. (2016)	●		●	≠	Species and acclimation duration
	Runge et al. (2016)			●	–	
	<b>Small et al. (2016)</b>		●		↓	
	<b>Waller et al. (2016)</b>		●		↓	
	<b>Wu et al. (2017)</b>		●			
	<b>Gooding et al. (2009)</b>	●			↑	Acclimation duration <i>p</i> CO <sub>2</sub> level and acclimation duration <i>p</i> CO <sub>2</sub> level <i>p</i> CO <sub>2</sub> level and acclimation duration
	Stumpp et al. (2011)	●		●	≠	
	Appelhans et al. (2012)		●	●	≠	
	<b>Burnell et al. (2013)</b>	●			↑	
	*Stumpp et al. (2013), Jager et al. (2016)	●		●	≠	
Appelhans et al. (2014)		●	●	≠	<i>p</i> CO <sub>2</sub> level and acclimation duration <i>p</i> CO <sub>2</sub> level	
<b>Keppel et al. (2015)</b>		●		↓		
<b>Carey et al. (2016)</b>			●	–		
<b>Kamya et al. (2016)</b>		●	●	≠		
Cnidaria (coral)	Houlbrègue et al. (2015)		●		↓	<i>p</i> CO <sub>2</sub> level
	<b>Towle et al. (2015)</b>	●			↑	

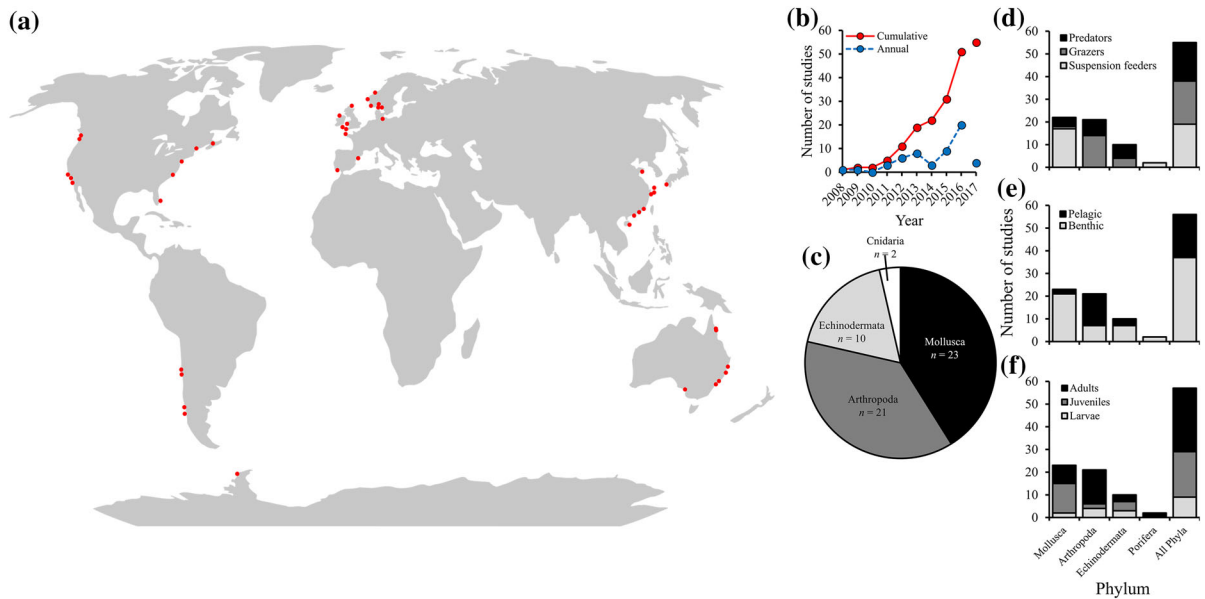
Bolded text denotes studies that assessed the effects of OA in the context of ocean warming. Studies are ordered chronologically (and then alphabetically) within each Phylum

\*Jager et al. (2016) used the feeding rate data from Stumpp et al. (2013) in a DEB model to derive feeding rates standardized for body size. The outcome reported here reflects the results from Fig. 3 (right panel) in Jager et al. (2016)

For overall outcomes: ↓ decreased feeding, ↑ increased feeding, – no change in feeding (null), ≠ mixed effects

under elevated CO<sub>2</sub>. No arthropod feeding strategies were affected (Fig. 4c). Data were lacking for suspension-feeding arthropods and echinoderms, as well as predatory molluscs (Fig. 4c); deposit feeders and scavengers were not found in our literature search. Habitat did not consistently affect feeding response to *p*CO<sub>2</sub>: benthic and pelagic molluscs and echinoderms displayed significantly reduced feeding rates under elevated CO<sub>2</sub> (Fig. 4d). Reduced feeding rate under elevated CO<sub>2</sub> was also observed for benthic and pelagic suspension feeders (Fig. 4e). With respect to acclimation time, significantly decreased feeding rates only occurred at *p*CO<sub>2</sub> levels < 1000 μatm, and for acclimation periods of 6–100 days (Fig. 5a, b). Interestingly, there was no significant positive effect of *p*CO<sub>2</sub> on feeding rate (Fig. 4a–e).

Differential effect sizes among a priori groups may have been impacted by varying *p*CO<sub>2</sub> levels if the *p*CO<sub>2</sub> ranges differed greatly among groups. For example, predators had significantly higher *p*CO<sub>2</sub> levels for elevated treatments than grazers and suspension feeders (ANOVA:  $F_{2,150} = 7.96$ ,  $p < 0.0005$ ), but their control *p*CO<sub>2</sub> levels were also higher. Two experiments were conducted on arthropods at extremely high *p*CO<sub>2</sub> levels (~ 9000 μatm; Dodd et al., 2015; Glandon & Miller, 2016). Although experimental *p*CO<sub>2</sub> levels in many of these studies were higher than the mean concentrations predicted by the IPCC for the year 2100, it is important to note that low pH and high *p*CO<sub>2</sub> are already experienced daily and seasonally by invertebrates living in estuaries, coasts, upwelling zones, and intertidal areas, and, thus,



**Fig. 1** **a** Map of approximate geographic locations of studies testing the effects of elevated  $p\text{CO}_2$  on marine calcifier feeding rates. **b** Cumulative ( $n = 55$ ) and annual publication counts for studies assessing the effects of elevated  $p\text{CO}_2$  on marine calcifier feeding rates found in our literature search. **c** The total number of studies assessing feeding rates in each of four calcifying Phyla. Pie slices represent the relative proportion of

each Phyla to the total number of studies found in our literature search. **d–f** The total number of studies assessing  $p\text{CO}_2$  effects on feeding rates across different feeding strategies (**c**), habitats (**d**), and life stages (**e**), for each of four calcifying Phyla. Note: The total number of studies across the four Phyla does not necessarily equal 55, as some studies may have employed > 1 divisive unit (i.e. Phyla, feeding strategy, habitat, or life stage)

were within reasonable ranges expected to be experienced by these animals in the next century. Another potentially confounding factor across studies was temperature. For example, many studies on arthropods were conducted at high latitudes, while studies on molluscs were conducted at a range of latitudes. Furthermore, temperature conditions in the experiments varied substantially. Since temperature has a large effect on metabolism, this could be an important interaction with OA impacts on feeding responses.

#### Predictors of calcifier feeding responses to elevated $\text{CO}_2$

AIC model selection revealed that of the 59 predictive models, “Phylum” best predicted effect size (Tables 3, S5). Based on delta AIC values, “life stage”, “exposure time”, and the null model (i.e. the model including experiment only) also served as top candidate models (Tables 3, S5).

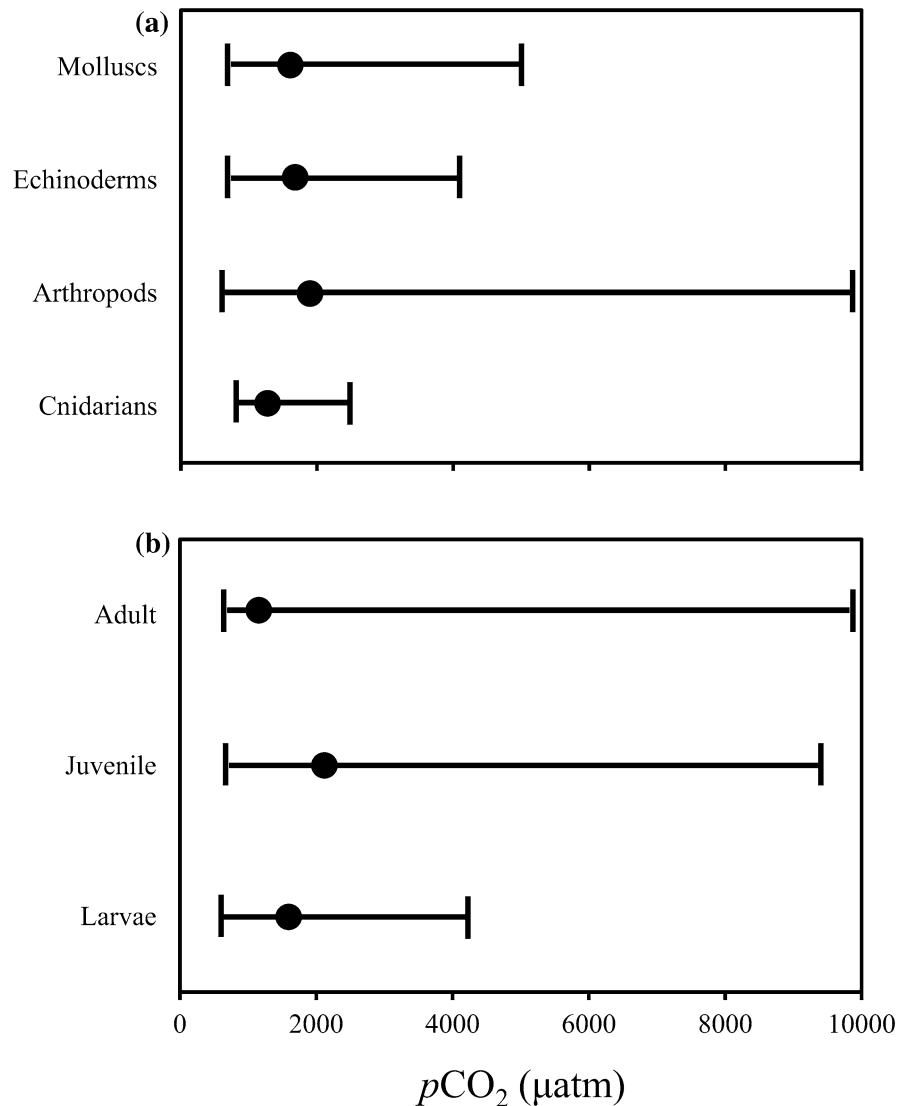
## Discussion

### Ocean acidification effects on calcifying invertebrate feeding rates

Our analysis of the literature indicates that ocean acidification effects on calcifier feeding are largely dependent on taxon (Phylum), life history stage, and duration of acclimation. Mollusc and echinoderm feeding appear to be sensitive to elevated  $p\text{CO}_2$ , particularly during early life history, while arthropod feeding appears more robust to elevated  $p\text{CO}_2$  effects. These results are in line with those of previous meta-analyses quantifying sensitivity in other biological endpoints (e.g. Kroeker et al., 2013; Wittman & Pörtner, 2013). Calcifying invertebrate feeding in response to elevated  $p\text{CO}_2$  also appears to be affected by acclimation duration, such that on average, acute acidification (< 10 days) had no effect, but longer-term exposure (> 10 days) did. Our meta-analysis also showed that exposure for more than 100 days did not significantly affect calcifier feeding, suggesting



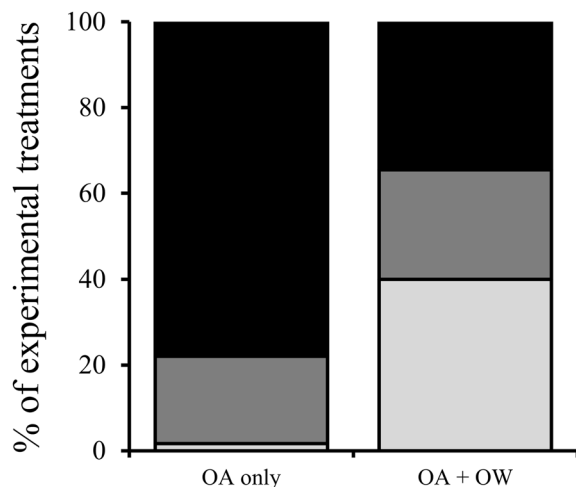
**Fig. 2** Ranges of experimental  $p\text{CO}_2$  conditions (i.e. ocean acidification treatments) encompassed by **a** each Phylum and **b** each life stage across the 55 studies assessing ocean acidification effects on marine calcifier feeding. Plots are means and error bars are minimum and maximum values



that exposure times beyond this may allow calcifiers to acclimate to elevated  $p\text{CO}_2$  conditions. Ultimately, our results suggest that feeding in molluscs and echinoderms may be more impacted by elevated  $p\text{CO}_2$  than arthropods, and that larvae and juveniles are more vulnerable than adults. Life stage was elucidated as the best predictor of effect size out of all fixed predictor variables, suggesting that larval and juvenile calcifiers are more susceptible to the effects of OA on feeding than adults. Analysis of interactive effects of life history stage and exposure duration was not possible, since early life history stages are short.

While our results suggest sensitivity of some taxa and life stages to OA, it is important to assess the

variability of effect sizes among the a priori groups that we defined to determine if significant mean effects are meaningful. After evaluation of experimental conditions, variation in effect size (defined by a significant  $Q$ -statistic) can be a secondary indicator of whether experimental results among studies are similar enough to justify combination (Hedges et al., 1999). We found that among-study variation in effect size was high for most groups and categories we chose (Phylum, Feeding Strategy, Habitat, Life Stage, Acclimation Time, Table S4). Adding a moderator such as “life stage” to the “Phylum” model decreased residual heterogeneity (fewer groups with significant  $Q$  tests, Table S4), indicating that life stage is likely an



**Fig. 3** The total number of experimental treatments ( $n = 59$ ) exhibiting increased (light grey bars), decreased (dark grey bars), and unaltered (i.e. null response; black bars) feeding rates in response to elevated  $p\text{CO}_2$  only (OA only) and elevated  $p\text{CO}_2$  + elevated temperature (OA + OW) from the 21 studies testing the combined effects of OA and OW on calcifier feeding rates

important moderator for the influence of Phylum on OA response. However, adding multiple moderators to the mixed effects models decreased the sample size of each category, over-parameterizing the models. We believe that for groups with a large sample size, a significant mean effect size, despite significant variability among its component studies, is robust. Ultimately, more experimental evidence testing for elevated  $\text{CO}_2$  effects on poorly represented groups is necessary.

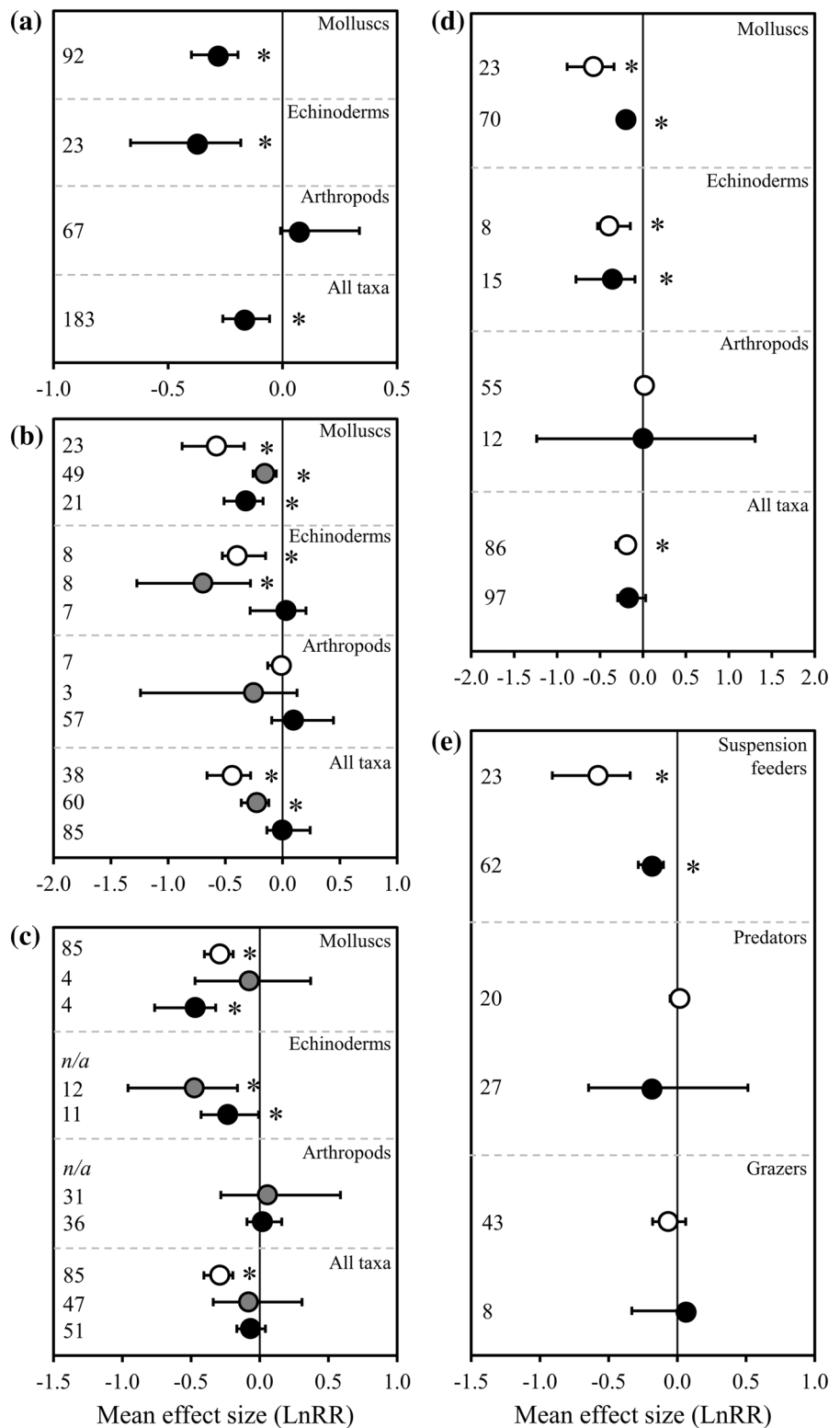
#### Mechanistic underpinnings of feeding rate responses to elevated $p\text{CO}_2$

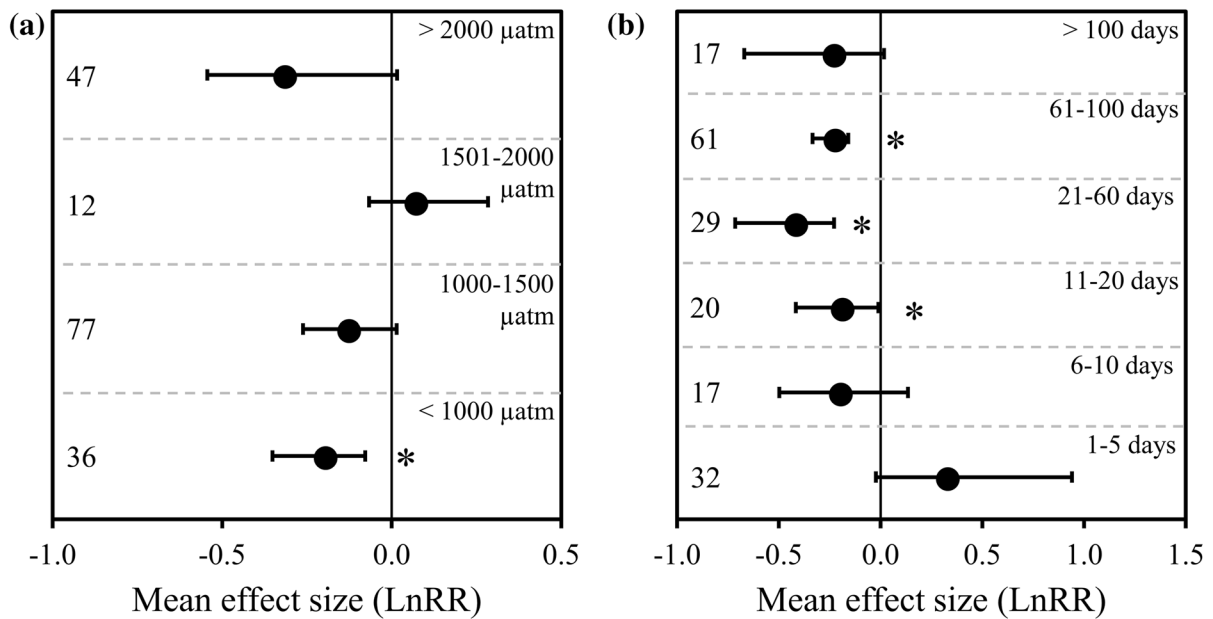
Where possible, we qualitatively examined feeding rates in context of accompanying physiological rates, such as respiration, excretion, and growth, to allow for a more comprehensive understanding of the impacts of elevated  $p\text{CO}_2$  on energetics. It was assumed that elevated  $p\text{CO}_2$  would be energetically costly to marine calcifying invertebrates, due to a combination of higher energy costs of biomineralization—especially when  $\text{CaCO}_3$  is corroded in acidic seawater (Palmer, 1992; Wood et al., 2008)—and higher energy allocation to homeostasis (Beniash et al., 2010). Homeostatic costs include ion and acid–base regulation, and

maintenance costs for protein synthesis (Pörtner, 2008). Remaining energy after homeostasis and maintenance may be used for growth and/or reproduction. A few feeding studies analysed the entire energy budget of calcifying marine invertebrates or measured enough pieces to make a few generalizations.

Animals could respond to increasing energy demands for homeostasis and/or biomineralization using a variety of generalized strategies, all of which have been noted in molluscs: (1) increasing aerobic respiration rates, increasing feeding rates to support increased metabolism, and increasing  $\text{NH}_4^+$  excretion rates as a result of increased metabolism (*Pinctada fucata* (Gould, 1850), Liu & He, 2012; *Argopecten purpuratus* (Lamarck, 1819), Ramajo et al., 2016a; Stapp et al., 2017); (2) increasing aerobic respiration rates, maintaining or decreasing feeding rates, and using catabolism to support increased energy demands, as evidenced by increased  $\text{NH}_4^+$  excretion rates (“tolerant” *Mytilus edulis* Linnaeus, 1758, Stapp et al., 2017); (3) maintaining respiration rates, maintaining or decreasing feeding rates, and using catabolism to support increased energy demands, as evidenced by increased excretion rates (*Mytilus galloprovincialis* Lamarck, 1819, Fernández-Reiriz et al., 2012; *Littorina littorea* (Linnaeus, 1758), Russell et al., 2013; *Ruditapes philippinarum* (Adams & Reeve, 1850), Xu et al., 2016); or (4) decreasing respiration and feeding rates, which often resulted in decreased growth/survival (*Ruditapes decussatus* (Linnaeus, 1758), Fernández-Reiriz et al., 2011; *Chlamys nobilis* (Reeve, 1852), Liu & He, 2012; *Perna viridis* (Linnaeus, 1758), Liu & He, 2012; *Mytilus chilensis* Hupé, 1854, Navarro et al., 2016; *Mytilus coruscus* Gould, 1861, Sui et al., 2016). Marine animals may use one of these strategies, or switch between them, depending on their physiological plasticity and length of acclimation. Thus, the strategies employed by calcifying marine invertebrates at different times may help to explain why feeding rates are depressed under elevated  $p\text{CO}_2$  in some cases, and not in others. Below, we use this framework to highlight potential Phyla-specific mechanisms for  $p\text{CO}_2$  effects on calcifier feeding rates, and provide additional hypotheses regarding mechanistic effects.

**Fig. 4** Summary of effect size analysis ( $n = 183$ ) for data organized by **a** taxa, **b** life stage within taxa (adult = black, juvenile = grey, larvae = white), **c** feeding strategy within taxa (grazers = black, predators = grey, suspension feeders = white), **d** habitat within taxa (benthic = black, pelagic = white), and **e** habitat within feeding strategy (benthic = black, pelagic = white). Numbers on left of each panel indicate the number of treatments used to derive the mean effect size. Error bars are upper and lower bootstrapped 95% confidence intervals. Asterisks indicate statistical significance (i.e. where 95% CI does not overlap with 0). Sample sizes do not match those of Table 1 because coral studies (Houlbrèque et al., 2015; Towle et al., 2015) were excluded, as well as two other studies—one that did not report variances (Watson et al., 2017) and one that contained negative means (Cooper et al., 2016)





**Fig. 5** Summary of effect size analysis for data organized by **a**  $p\text{CO}_2$  level, and **b** acclimation duration. Numbers on left of each panel indicate the number of treatments used to derive the

mean effect size. Error bars are upper and lower bootstrapped 95% confidence intervals. Asterisks indicate statistical significance (i.e. where 95% CI does not overlap with 0)

**Table 3** Top candidate models from AIC model selection of additive linear mixed effects models incorporating the effects of phylum, feeding strategy, habitat, life stage, acclimation time, and  $p\text{CO}_2$  level of effect size (LnRR)

Model	$K$	AICc	$\Delta\text{AICc}$	AICcWt	Cum.Wt	Res.LogLik
Phylum	5	431.85	0.00	0.21	0.21	– 210.76
Life stage	6	432.40	0.55	0.16	0.37	– 209.96
Experiment	3	432.46	0.61	0.15	0.52	– 213.16
Exposure time	9	433.34	1.49	0.10	0.62	– 207.15

All models incorporated experiment as a random effect. Full AIC results can be found in Table S5

### Molluscs

Since bivalves are osmoconformers (Shumway, 1977), they have reduced capacity for acid–base regulation compared to other species, which may explain their increased sensitivity to elevated  $p\text{CO}_2$  (Gazeau et al., 2013). Bivalve and echinoderm growth, respiration, and other physiological processes are more sensitive to elevated  $p\text{CO}_2$  than more metabolically active teleost fishes and decapod crustaceans, due to their lack of respiratory pigments (Melzner et al., 2009). Bivalves compensate for acidosis by increasing bicarbonate through dissolution of shell  $\text{CaCO}_3$  and through amino acid catabolism

(Michaelidis et al., 2005); thus, loss of shell mass and excretion of  $\text{NH}_4^+$  can be indicators of acidosis. Early shell formation may not be energy-limited, due to maternal-derived energy reserves (Frieder et al., 2017), and shell and soft tissue development may be uncoupled (Waldbusser et al., 2015), or shell dissolution in larval stages could result in mechanical alterations to the shell that eventually affect feeding and energy input (Talmage & Gobler, 2010). Elevated  $p\text{CO}_2$  increased ADP:ATP levels in one study on juvenile oysters (Beniash et al., 2010), but did not affect overall ATP levels in another study; however, lipid and glycogen stores were reduced to maintain cellular energy status (Dickinson et al., 2012).

Suspension feeding is an energy-demanding process controlled by ciliary activity on the gill (Galtsoff, 1964; Jorgensen, 1990), and is commonly used as an indicator of environmental stress (Axiak & George, 1987; Stevens, 1987). Ciliary activity requires a large amount of energy (*Mytilus edulis* ATP hydrolysis 58–87% of ATP synthesized; Clemmesen & Jorgensen 1987), and is mechanically linked to respiration. In bivalves, the GABA<sub>A</sub> (or GABA<sub>A</sub>-like) neuroreceptor can underlie behavioural responses to elevated concentrations of  $p\text{CO}_2$  in sediments (Clements et al., 2017). GABA has been suggested to play an inhibitory role in regulating the actions of serotonin on ciliary beating (Mathieu et al., 2014). In gastropods, GABA<sub>A</sub> (or GABA<sub>A</sub>-like) functioning is also linked to prey escape responses to predators, and could thus be important in predator feeding rates (Watson et al., 2014). While GABA<sub>A</sub> receptors appear sensitive to  $p\text{CO}_2$  elevation in molluscs, the same receptors in larval crustaceans appear robust to elevated  $p\text{CO}_2$  (Charpentier & Cohen, 2016). Consequently, altered ion gradients at GABA<sub>A</sub> (or GABA<sub>A</sub>-like) receptors resulting from elevated  $\text{CO}_2$  may act to drive many of the effects on calcifier feeding.

#### Echinoderms

Biological responses of echinoderms to OA are class- and species-specific (Dupont et al., 2010). In our study, differences appeared to depend on local adaptation and the relative need for calcification. For example, among sea stars, feeding rates in *Asterias rubens* Linnaeus, 1758 appeared to be more sensitive to  $p\text{CO}_2$  than those of *Pisaster ochraceus* (Brandt, 1835), but *P. ochraceus* may be better adapted to high  $p\text{CO}_2$  since it lives in the intertidal in an upwelling zone (Keppel et al., 2015). Mechanistically, some echinoderms can resist the effect of OA on calcification due to a protective organic layer around their spines (Ries et al., 2009), or by buffering using their magnesium-calcite test (Miles et al., 2007), which may invoke physiological trade-offs that reduce feeding rates and other physiological rates such as respiration. Elevated  $p\text{CO}_2$  can also affect the feeding structures of grazing echinoderms (e.g. sea urchins' Aristotle's lantern), although it appears that OA effects on these structures may be dependent on diet (Asnaghi et al., 2013). Furthermore, olfactory changes under elevated  $p\text{CO}_2$  may also be responsible for the observed

negative effects on echinoderm predation rates, given that olfaction is particularly susceptible to changes in  $p\text{CO}_2$  (Clements & Hunt, 2015; Ashur et al., 2017; Tresguerres & Hamilton, 2017). Fewer feeding studies were conducted on echinoderms compared to molluscs, and fewer still included respiration measurements, precluding associations between feeding and respiration. A distinct mechanism(s) for  $p\text{CO}_2$  effects on echinoderm feeding rates requires more detailed investigation.

#### Arthropods

In contrast to molluscs and echinoderms, arthropod feeding appeared less affected by elevated  $p\text{CO}_2$ . This observation may be due to differences in metabolic rates, the use of respiratory pigments in arthropods, and/or acid–base regulation (Melzner et al., 2009). Regulation of extracellular pH in arthropods such as *Carcinus maenas* (Linnaeus, 1758) may allow these crabs to feed at normal rates during short-term assays (Appelhans et al., 2012), but may increase energy demands during longer-term exposure. Likewise, a variety of copepod species can strongly regulate internal pH without requiring additional energy via feeding (e.g. Hildebrandt et al., 2016). However, while arthropods can regulate extracellular pH, effects of acidification on feeding rates and, thus, energy balance appear to be mixed. For example, most copepod feeding was unaffected by  $p\text{CO}_2$ , while feeding of crabs, lobsters, and shrimp was most often negatively affected. Growth rates are complicated to measure in arthropods, due to moulting, but where lower growth was noted, respiration rates were also often negatively affected (e.g. *Euphausia pacifica* Hansen, 1911, Cooper et al., 2016; *Homarus gammarus* (Linnaeus, 1758), Small et al., 2016). Respiration rates of copepods under elevated  $p\text{CO}_2$  appeared to be sex-specific (Cripps et al., 2016) and respond to food concentrations (Thor & Oliva, 2015), and thus may lend to the variable responses observed in arthropods. A direct mechanism for  $p\text{CO}_2$  effects on the feeding rates of arthropod species requires more research.

#### Corals

Unlike the other taxa included in our meta-analysis, there exists a relative paucity of information on feeding rate responses of corals to OA, precluding

any meaningful conclusions. The two studies measuring coral feeding rates under elevated  $p\text{CO}_2$  identified in this review found contrasting effects of OA on coral feeding rates. Houlbrèque et al. (2015) reported reduced feeding rates under elevated  $p\text{CO}_2$  in *Stylophora pistillata* Esper, 1797. Interestingly, however, these authors found that depressed feeding did not impact physiology or calcification, so long as the corals were consuming food at any rate. In contrast, Towle et al. (2015) reported increased feeding rates for *Acropora cervicornis* (Lamarck, 1816), which likely mitigated OA effects on calcification. Together, these studies suggest that food consumption in corals, despite potentially being reduced under elevated  $p\text{CO}_2$ , can mitigate OA effects on calcification for these two species, and that reduced feeding may not necessarily result in negative physiological effects. This idea is further supported by Edmunds (2011), who reported that food consumption partially alleviated OA effects on growth in *Porites* spp. Link, 1807. More research is necessary to draw more confident conclusions, however, given that only two studies measuring coral feeding rates were found in our literature search.

#### Recommendations for future research

This quantitative review has identified knowledge gaps and opportunities for research in key areas that would aid in development of broader understanding of physiological causes, and widespread ecological effects, of OA on the feeding rates of marine calcifying invertebrates.

#### Population effects

Global marine change research has recently started to focus on the potential for organisms to acclimate and/or adapt to global change stressors across multiple generations (Harvey et al., 2014; Sunday et al., 2014; Calosi et al., 2016). While such studies have been implemented for many biological endpoints, we did not find studies testing for acclamatory or adaptive responses of marine calcifier feeding rates to elevated  $\text{CO}_2$ . These studies are needed to realistically predict effects of global marine change stressors on the population scale.

#### Community effects

Our results indicate that elevated  $p\text{CO}_2$  can impact the feeding performance of certain marine calcifiers; next steps would be to examine interactive effects of  $p\text{CO}_2$  on both the prey and the consumer. Many studies consider the effects of prey exposure (e.g. Amaral et al., 2012; Rossoll et al., 2012; Benítez et al., 2016; Duarte et al., 2016; Dupont et al., 2015; Isari et al., 2016) and consumer exposure (studies included in this review) in isolation; however, combined effects on predator–prey and herbivore–plant interactions can have major implications for predicting community-level responses to elevated  $p\text{CO}_2$ . For example, while elevated  $\text{CO}_2$  appeared to affect individual attributes of a crab predator (*Carcinus maenas*) and its gastropod prey (*Littorina littorea*), the predator–prey interactions between these two species were unaltered (Landes & Zimmer, 2012). In contrast, elevated  $\text{CO}_2$  reduced growth in the barnacle *Semibalanus balanoides* (Linnaeus, 1767), but alterations in the feeding behaviour of its gastropod predator, *Nucella lapillus* (Linnaeus, 1758), dominated the relationship and snails reduced feeding rates to the point of starvation (Harvey & Moore, 2017). It is thus evident that considering elevated  $p\text{CO}_2$  effects to both the consumer and its food are important when testing for relative effects of OA on marine calcifier feeding performance.

#### Functional and ecological consequences of altered feeding rates

Taxon- and life stage-specific effects of elevated  $p\text{CO}_2$  on feeding rates of calcifying marine invertebrates may lead to functional changes in populations, communities, and ecosystems. Where feeding rates are depressed under elevated  $p\text{CO}_2$ , organisms may not be able acquire the necessary energy to overcome the negative physiological consequences of OA. As such, population declines might be expected in organisms suffering depressed feeding rates from elevated  $p\text{CO}_2$ . Population-level changes can also accompany elevated feeding rates under OA, as increased feeding may enhance populations of certain organisms, or lead to faster depletion of their prey or competitors. Such effects could have major implications for the carrying capacity of populations in which feeding rates increase, and shifts in community structure occur.



## Additional considerations for future studies

### *Multiple stressor effects*

Although it appears that CO<sub>2</sub>-induced OA can impact the feeding rates of some calcifying marine invertebrates, it is important to understand that OA is unlikely to occur in isolation, but will occur in the wake of numerous other stressors of global marine change such as salinity changes, ocean warming (OW), and hypoxia (Breitburg et al., 2015). The complex interactions between these multiple drivers can thus elicit different biological responses than the responses observed in single-stressor experiments (Kroeker et al., 2013; Harvey et al., 2013; Gobler & Baumann, 2016). Our literature search identified a total of 21 studies assessing the effects of elevated pCO<sub>2</sub> on feeding rates in the context of elevated temperature consistent with OW predictions (i.e.  $\leq +5^{\circ}\text{C}$  warming; Table 2). While this sample size is too low to assess meta-analytically, a comparison of statistical outcomes between OA only treatments and OA + OW treatments in those 21 studies revealed that OA + OW treatments resulted in a far higher percentage of increased feeding rates than of null responses, while the percentage of decreased feeding responses remained the same (Fig. 3). Thus, it appears that OW may act to predominantly increase calcifier feeding rates in an antagonistic fashion with OA, although this effect may not be sufficient to overcome feeding rate decreases associated with OA. Other anthropogenic changes such as eutrophication and food availability are important to consider in the context of OA (Thomsen et al., 2013; Wallace et al., 2014; Pan et al., 2015; Ramajo et al., 2016a, b), particularly given the high degree of temporal variability of such conditions in coastal and estuarine waters. In a multiple stressor study on feeding rates, Cole et al. (2016) tested for the combined effects of OA, OW, hyposalinity, and food availability on the feeding rates of the oyster *Ostrea angasi* Sowerby II, 1871, reporting that oysters were unable to compensate for increases in metabolic demand by feeding more under stressed conditions. Testing a similar number of stressors, Burnell et al. (2013) assessed the effect of elevated pCO<sub>2</sub> on the feeding rate of the sea urchin, *Amblypneustes pallidus* (Lamarck, 1816), in the context of OW and eutrophication, reporting that eutrophication offset increased feeding (grazing) rates

imposed by OA and OW. Campanati et al. (2016) reported that barnacles, *Balanus amphitrite* Darwin, 1854, increased feeding rates under elevated pCO<sub>2</sub> and reduced O<sub>2</sub>. In contrast, Sui et al. (2016) reported that elevated pCO<sub>2</sub> reduced feeding rates in the mussel *Mytilus coruscus* under ambient (but not reduced) O<sub>2</sub> levels, and that low O<sub>2</sub> alone elicited an even more severe decrease in mussel feeding rate than elevated pCO<sub>2</sub> alone. Ultimately, the number of studies assessing the effects of OA on marine calcifier feeding rates in the context of other global change stressors in the marine realm is low, especially for stressors such as salinity, oxygen and food availability that are common stressors in coastal and estuarine areas.

### *Acclimation and adaptation potential*

Alongside testing the effects of multiple stressors, global marine change research has recently started to focus on the potential for organisms to acclimate and/or adapt to global change stressors across multiple generations (Harvey et al., 2014; Sunday et al., 2014; Calosi et al., 2016). While such studies have been implemented for many biological endpoints, we did not identify any studies testing for acclimatory or adaptive responses of marine calcifier feeding rates to elevated pCO<sub>2</sub>. Given that such studies are crucial to realistically predicting effects of marine global change stressors, studies assessing the adaptive and plastic capacity for marine calcifiers to adequately alter their feeding rates in response to global change stressors across multiple generations are most certainly needed.

### *Food exposure versus feeder exposure to elevated pCO<sub>2</sub>*

While our results suggest that elevated pCO<sub>2</sub> can impact the feeding performance of certain calcifying marine invertebrates, the studies herein often do not consider the combined effects of exposure to elevated pCO<sub>2</sub> in both the prey and the consumer. While studies often consider the effects of prey or food exposure (e.g. Amaral et al., 2012; Rossoll et al., 2012; Dupont et al., 2015; Benítez et al., 2016; Duarte et al., 2016; Isari et al., 2016; Smith et al., 2016) and consumer exposure (studies highlighted in this review) in isolation, the combined effects of prey and consumer exposure are most often ignored. However, this

consideration can have major implications for predicting feeding rate responses to elevated  $p\text{CO}_2$ . Moreover, considering the effect of OA on both consumers and prey is an important consideration when attempting to predict community responses to elevated  $p\text{CO}_2$ . For example, while elevated  $p\text{CO}_2$  appeared to affect individual attributes of a crab predator (*Carcinus maenas*) and its gastropod prey (*Littorina littorea*), the predator–prey interactions and outcomes between these two species were unaltered (Landes & Zimmer, 2012). In contrast, OA effects on crab (*Panopeus herbstii* H. Milne Edwards, 1834) foraging behaviour outweighed OA effects on its oyster prey (*Crassostrea virginica* (Gmelin, 1791)) in driving feeding rate responses to OA (Dodd et al., 2015). Similarly, while elevated  $p\text{CO}_2$  reduced tissue production and rostro-carinal diameter in the barnacle *Semibalanus balanoides*, alterations in the feeding behaviour of its gastropod predator, *Nucella lapillus*, dominated the relationship and snails reduced feeding rates to the point of starvation (Harvey & Moore, 2017). It is thus evident that considering effects to both the consumer and its prey are important when testing for effects of OA on marine calcifier feeding performance.

#### *Incorporating other processes involved in energy acquisition*

It is important to note that feeding rates may not always correspond directly with energy acquisition. Other processes of energy acquisition such as appetite, digestion, assimilation efficiency, and energy allocation are also at play, along with behavioural processes such as food selectivity and foraging and handling times (among others). Furthermore, effects of elevated  $p\text{CO}_2$  on energetically demanding processes also need to be accounted for. Thus, studies focusing on more direct measures of energy acquisition will be useful for determining the extent to which animals can use increased energy acquisition to overcome negative effects of  $\text{CO}_2$ -induced OA. While such studies have been recently conducted (e.g. Stumpp et al., 2013; Morley et al., 2016; Yuan et al., 2016; Harvey & Moore, 2017), our knowledge to this extent is still emerging and awaits a more established body of research.

## Conclusion

Our quantitative study highlights the importance of taxon and life stage when predicting OA effects on the feeding performance of calcifying marine invertebrates. Mollusc and echinoderm feeding rates—particularly at early life stages—are sensitive to elevated  $p\text{CO}_2$  conditions at exposure times of 10–100 days; arthropod feeding appears robust to elevated  $p\text{CO}_2$ . Physiological, mechanical, and/or neurobiological changes induced by OA may help to mechanistically explain observed effects of elevated  $p\text{CO}_2$  on invertebrate feeding rates; however, more research is necessary in order to draw more confident conclusions. How feeding rates are impacted when both consumer and food are exposed to elevated  $p\text{CO}_2$  is a key area for future research. Knowledge of the effects of local adaptation and acclimation, multiple stressors, and functional and ecological consequences of changes in feeding rates are also needed to understand what such changes mean for future ecosystems under global change.

**Acknowledgements** We wish to thank Dr. Benjamin Harvey for his assistance and guidance with the meta-analysis component of this study. We also thank Dr. Robert Condon, Dr. Luc Comeau, Dr. Remi Sonier, and three anonymous reviewers for constructive feedback which helped improve the original manuscript. This study was funded by a NSERC Visiting Postdoctoral Fellowship to JCC (Grant #501540-2016).

## References

- Amaral, V., H. N. Cabral & M. J. Bishop, 2012. Effects of estuarine acidification on predator–prey interactions. *Marine Ecology Progress Series* 445: 117–127.
- Anderson, D. R., 2007. *Model Based Inference in the Life Sciences: A Primer on Evidence*. Springer, New York.
- Appelhans, Y. S., J. Thomsen, C. Pansch, F. Melzner & M. Wahl, 2012. Sour times: seawater acidification effects on growth, feeding behaviour, and acid-base status of *Asterias rubens* and *Carcinus maenas*. *Marine Ecology Progress Series* 459: 85–97.
- Appelhans, Y. S., J. Thomsen, S. Opitz, C. Pansch, F. Melzner & M. Wahl, 2014. Juvenile sea stars exposed to acidification decrease feeding and growth with no acclimation potential. *Marine Ecology Progress Series* 509: 227–239.
- Arnberg, M., P. Calosi, J. I. Spicer, A. H. S. Tandberg, M. Nilsen, S. Westerlund & R. K. Bechmann, 2013. Elevated temperature elicits greater effects than decreased pH on the development, feeding and metabolism of northern shrimp (*Pandalus borealis*) larvae. *Marine Biology* 160: 2037–2048.

- Ashur, M. M., N. K. Johnston & D. L. Dixon, 2017. Impacts of ocean acidification on sensory function in marine organisms. *Integrative and Comparative Biology* 57: 63–80.
- Asnaghi, V., M. Chiantore, L. Mangialajo, F. Gazeau, P. Francour, S. Alliouane & J.-P. Gattuso, 2013. Cascading effects of ocean acidification in a rocky subtidal community. *PLoS ONE* 8: e61978.
- Axiak, V. & J. J. George, 1987. Effects of exposure to petroleum hydrocarbons in the gill functions and ciliary functions of a marine bivalve. *Marine Biology* 94: 241–249.
- Beniash, E., A. Ivanina, N. S. Lieb, I. Kurochkin & I. M. Sokolova, 2010. Elevated level of carbon dioxide affects metabolism and shell formation in oysters *Crassostrea virginica*. *Marine Ecology Progress Series* 419: 95–108.
- Benítez, S., C. Duarte, J. López, P. H. Manríquez, J. M. Navarro, C. C. Bonta, R. Torres & P. Quijón, 2016. Ontogenetic variability in the feeding behavior of a marine amphipod in response to ocean acidification. *Marine Pollution Bulletin* 112: 375–379.
- Breitburg, D. L., N. Steinberg, S. DuBeau, C. Cooksey & E. D. Houde, 1994. Effects of low dissolved oxygen on predation on estuarine fish larvae. *Marine Ecology Progress Series* 104: 235–246.
- Breitburg, D. L., J. Salisbury, J. M. Bernhard, et al., 2015. And on top of all that... coping with ocean acidification in the midst of many stressors. *Oceanography* 28: 48–61.
- Burnell, O. W., B. D. Russell, A. D. Irving & S. D. Connell, 2013. Eutrophication offsets increased sea urchin grazing on seagrass caused by ocean warming and acidification. *Marine Ecology Progress Series* 485: 37–46.
- Burnham, K. P. & D. R. Anderson, 2002. *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Burton-Sanders, M., T. P. Bean, T. H. Hutchinson & W. J. F. Le Quesne, 2013. Juvenile king scallop, *Pecten maximus*, is potentially tolerant to low levels of ocean acidification when food is unrestricted. *PLoS One* 8: e74118.
- Cai, W., X. Hu, W. Huang, M. Murrell, J. Lehrter, S. Lohrenz, W. Chou, W. Zhai, J. Hollibaugh, Y. Wang, P. Zhao, X. Guo, K. Gundersen, M. Dai & G. Gong, 2011. Acidification of subsurface coastal waters enhanced by eutrophication. *Nature Geoscience* 4: 766–770.
- Caldeira, K. & M. E. Wickett, 2003. Anthropogenic carbon and ocean pH. *Nature* 425: 365.
- Calosi, P., P. DeWit, P. Thor & S. Dupont, 2016. Will life find a way? Evolution of marine species under global change. *Evolutionary Applications* 9: 1035–1042.
- Campanati, C., S. Yip, A. Lane & V. Thiyagarajan, 2016. Combined effects of low pH and low oxygen on the early-life stages of the barnacle *Balanus amphitrite*. *ICES Journal of Marine Science* 73: 791–802.
- Carey, N., J. Harionto & M. Byrne, 2016. Sea urchins in a high-CO<sub>2</sub> world: partitioned effects of body size, ocean warming and acidification on metabolic rate. *Journal of Experimental Biology* 219: 1178–1186.
- Chaparro, O. R., Y. A. Montiel, C. J. Segura, V. M. Cubillos, R. J. Thompson & J. M. Navarro, 2008. The effect of salinity on clearance rate in the suspension-feeding estuarine gastropod *Crepidatella dilatata* under natural and controlled conditions. *Estuarine, Coastal and Shelf Science* 74: 861–868.
- Charpentier, C. L. & J. H. Cohen, 2016. Acidification and  $\gamma$ -aminobutyric acid independently alter kairomone-induced behaviour. *Royal Society Open Science* 3: 160311.
- Christmas, A. M. F. 2013. Effects of ocean acidification on dispersal behavior in the larval stage of the Dungeness crab and the Pacific Green Shore crab. MSc thesis, Western Washington University, Bellingham, WA, USA. 72 pp. <http://cedar.wvu.edu/cgi/viewcontent.cgi?article=1305&context=wwuet> (last accessed 02 August 2017).
- Clements, J. C. & H. L. Hunt, 2015. Marine animal behaviour in a high CO<sub>2</sub> world. *Marine Ecology Progress Series* 536: 259–279.
- Clements, J. C., M. M. Bishop & H. L. Hunt, 2017. Elevated temperature has adverse effects on GABA-mediated avoidance behaviour to sediment acidification in a wide-ranging marine bivalve. *Marine Biology* 164: 56.
- Clemmesen, B. & C. B. Jørgensen, 1987. Energetic costs and efficiencies of ciliary filter feeding. *Marine Biology* 94: 445–449.
- Cole, V. J., L. M. Parker, S. J. O'Connor, W. A. O'Connor, E. Scanes, M. Byrne & P. M. Ross, 2016. Effects of multiple climate change stressors: ocean acidification interacts with warming, hyposalinity, and low food supply on the larvae of the brooding flat oyster *Ostrea angasi*. *Marine Biology* 163: 125.
- Cooper, H. L., D. C. Potts & A. Paytan, 2016. Metabolic responses of the North Pacific krill, *Euphausia pacifica*, to short- and long-term pCO<sub>2</sub> exposure. *Marine Biology* 163: 207.
- Cripps, G., K. J. Flynn & P. K. Lindeque, 2016. Ocean acidification affects the phyto-zoo plankton trophic transfer efficiency. *PLoS One* 11: e0151739.
- Dickinson, G. H., A. V. Ivanina, O. B. Matoo, H. O. Pörtner, G. Lannig, C. Bock, E. Beniash & I. M. Sokolova, 2012. Interactive effects of salinity and elevated CO<sub>2</sub> levels on juvenile eastern oysters, *Crassostrea virginica*. *Journal of Experimental Biology* 215: 29–43.
- Dodd, L. F., J. H. Grabowski, M. F. Piehler, I. Westfield & J. B. Ries, 2015. Ocean acidification impairs crab foraging behaviour. *Proceedings of the Royal Society B: Biological Sciences* 282: 20150333.
- Duarte, C., I. Hendriks, T. Moore, Y. Olsen, A. Steckbauer, L. Ramajo, J. Carstensen, J. Trotter & M. McCulloch, 2013. Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. *Estuaries and Coasts* 36: 221–236.
- Duarte, C., J. López, S. Benítez, P. H. Manríquez, J. M. Navarro, C. C. Bonta, R. Torres & P. Quijón, 2016. Ocean acidification induces changes in algal palatability and herbivore feeding behavior and performance. *Oecologia* 180: 453–462.
- Dupont, S., O. Ortega-Martínez & M. Thorndyke, 2010. Impact of near-future ocean acidification on echinoderms. *Ecotoxicology* 19: 449–462.
- Dupont, S. T., M. Murcurio, A. A. G. Giacoletti, et al., 2015. Functional consequences of prey acclimation to ocean acidification for the prey and its predator. *PeerJ Preprints*. <https://doi.org/10.7287/peerj.preprints.1438v1>.

- Edmunds, P. J., 2011. Zooplanktivory ameliorates the effects of ocean acidification on the reef coral *Porites* spp. *Limnology and Oceanography* 56: 2402–2410.
- Fernández-Rieriz, M. J., P. Range, X. A. Álvarez-Saldago & U. Labarta, 2011. Physiological energetics of juvenile clams *Ruditapes decussatus* in a high CO<sub>2</sub> coastal ocean. *Marine Ecology Progress Series* 433: 97–105.
- Fernández-Reiriz, F., P. Range, X. A. Álvarez-Salgado, J. Espinosa & U. Labarta, 2012. Tolerance of juvenile *Mytilus galloprovincialis* to experimental seawater acidification. *Marine Ecology Progress Series* 454: 65–74.
- Frieder, C. A., S. L. Applebaum, T.-C. F. Pan, D. Hedgecock & D. T. Manahan, 2017. Metabolic cost of calcification in bivalve larvae under experimental ocean acidification. *ICES Journal of Marine Science* 74: 941–954.
- Galtsoff, P. S., 1964. The American oyster *Crassostrea virginica* Gmelin. *Fisheries Bulletin of the Fish and Wildlife Service of the US* 64: 1–480.
- Gazeau, F., L. M. Parker, S. Comeau, J.-P. Gattuso, W. A. O'Connor, S. Martin, H.-O. Pörtner & P. M. Ross, 2013. Impacts of ocean acidification on marine shelled molluscs. *Marine Biology* 160: 2207–2245.
- Glandon, H. L. & T. J. Miller, 2016. No effect of high pCO<sub>2</sub> on juvenile blue crab, *Callinectes sapidus*, growth and consumption despite positive responses to concurrent warming. *ICES Journal of Marine Science* 74: 1201–1209.
- Gobler, C. J. & H. Baumann, 2016. Hypoxia and acidification in ocean ecosystems: coupled dynamics and effects on marine life. *Biology Letters* 12: 20150976.
- Gooding, R., C. Harley & E. Tang, 2009. Elevated water temperature and carbon dioxide concentration increase the growth of a keystone echinoderm. *Proceedings of the National Academy of Sciences of the USA* 106: 9316–9321.
- Harvey, B. P. & P. J. Moore, 2017. Ocean warming and acidification prevent compensatory response in a predator to reduced prey quality. *Marine Ecology Progress Series* 563: 111–122.
- Harvey, B. P., D. Gwynn-Jones & P. J. Moore, 2013. Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecology and Evolution* 3: 1016–1030.
- Harvey, B. P., A.-J. Balsam, S. Broszeit, et al., 2014. Evolution of marine organisms under climate change at different levels of biological organisation. *Water* 6: 1545–1574.
- Hedges, L. V., J. Gurevitch & P. S. Curtis, 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80: 1150–1156.
- Hendriks, I. E., C. B. Duarte & M. Álvarez, 2010. Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuarine, Coastal, and Shelf Science* 86: 157–164.
- Hildebrandt, N., F. J. Sartoris, K. G. Schulz, U. Riebsell & B. Niehoff, 2016. Ocean acidification does not alter grazing in the calanoid copepods *Calanus finmarchicus* and *Calanus glacialis*. *ICES Journal of Marine Science* 73: 927–936.
- Hoegh-Guldberg, O., R. Cai, E. S. Poloczanska, et al. 2014. The ocean. In Barros, V. R., Field, C. B., Dokken, D. J., et al. (eds), *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Cambridge University Press, New York: 1655–1731.
- Hofmann, G. E., J. P. Barry, P. J. Edmunds, R. D. Gates, D. A. Hutchins, T. Klinger & M. A. Sewell, 2010. The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective. *Annual Reviews of Ecology, Evolution and Systematics* 41: 127–147.
- Houlbrèque, F., S. Reynaud, C. Godinot, F. Oberhänsli, R. Rodolfo-Metalpa & C. Ferrier-Pagès, 2015. Ocean acidification reduces feeding rates in the scleractinian coral *Stylophora pistillata*. *Limnology and Oceanography* 60: 89–99.
- Howes, E. L., F. Joos, C. M. Eakin & J.-P. Gattuso, 2015. An updated synthesis of the observed and projected impacts of climate change on the chemical, physical and biological processes in the oceans. *Frontiers in Marine Science* 2: 36.
- Isari, S., S. Zervoudaki, E. Siaz, C. Pelejero & J. Peters, 2015. Copepod vital rates under CO<sub>2</sub>-induced acidification: a calanoid species and a cyclopoid species under short-term exposures. *Journal of Plankton Research* 37: 912–922.
- Isari, S., S. Zervoudaki, J. Peters, G. Papantoniou, C. Pelejero & E. Siaz, 2016. Lack of evidence for elevated CO<sub>2</sub>-induced bottom-up effects on marine copepods: a dinoflagellate–calanoid prey–predator pair. *ICES Journal of Marine Science* 73: 650–658.
- Jager, T., E. Ravagnan & S. Dupont, 2016. Near-future ocean acidification impacts maintenance costs in sea-urchin larvae: identification of stress factors and tipping points using a DEB modelling approach. *Journal of Experimental Marine Biology and Ecology* 474: 11–17.
- Jorgensen, C. B., 1990. *Bivalve Filter Feeding: Hydrodynamics, Bioenergetics, Physiology, and Ecology*. Olsen and Olsen, Fredensborg: 140.
- Kamya, P. Z., M. Byrne, A. Graba-Landry & S. A. Dworjanyn, 2016. Near-future ocean acidification enhances the feeding rate and development of the herbivorous juveniles of the crown-of-thorns starfish, *Acanthaster planci*. *Coral Reefs* 35: 1241–1251.
- Keppel, E. A., R. A. Scrosati & S. C. Courtenay, 2015. Interactive effects of ocean acidification and warming on subtidal mussels and sea stars from Atlantic Canada. *Marine Biology Research* 11: 337–348.
- Ko, W. K. G., B. S. V. Chan, R. Dineshram, K. S. D. Choi, J. A. Li, Z. Yu & V. Thiagarajan, 2013. Larval and post-larval stages of pacific oyster (*Crassostrea gigas*) are resistant to elevated CO<sub>2</sub>. *PLoS ONE* 8: e64147.
- Kooijman, S. A. L. M., 2009. *Dynamic Energy Budget Theory for Metabolic Organisation*. Cambridge University Press, Cambridge.
- Kroeker, K. J., R. L. Kordas, R. Crim, I. E. Hendriks, L. Ramajo, G. S. Singh, C. M. Duarte & J.-P. Gattuso, 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology* 19: 1884–1896.
- Kurihara, H., M. Matsui, H. Furukawa, M. Hayashi & A. Ishimatsu, 2008. Long-term effects of predicted future seawater CO<sub>2</sub> conditions on the survival and growth of the marine shrimp *Palaemon pacificus*. *Journal of Experimental Marine Biology and Ecology* 367: 41–46.
- Lajeunesse, M. J. & M. R. Forbes, 2003. Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. *Ecology Letters* 6: 448–454.

- Landes, A. & M. Zimmer, 2012. Acidification and warming affect both a calcifying predator and prey, but not their interaction. *Marine Ecology Progress Series* 450: 1–10.
- Lankford Jr., T. E. & T. E. Targett, 1994. Suitability of estuarine nursery zones for juvenile weakfish (*Cynoscion regalis*): effects of temperature and salinity on feeding, growth and survival. *Marine Biology* 119: 611–620.
- Le Moullac, G., C. Soyeux, O. Latchere, J. Vidal-Dupio, J. Fremerly, D. Saulnier, A. L. Yat, C. Belliard, N. Mazouni-Gaertner & Y. Gueguen, 2016. *Pinctada margaritifera* responses to temperature and pH: acclimation capabilities and physiological limits. *Estuarine, Coastal and Shelf Science* 182B: 261–269.
- Lefevre, S. J. 2016. Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated temperature, high CO<sub>2</sub> and their interaction. *Conservation Physiology* 4: cow009. <https://doi.org/10.1093/conphys/cow009>
- Li, W. & K. Gao, 2012. A marine secondary producer respire and feeds more in a high CO<sub>2</sub> ocean. *Marine Pollution Bulletin* 64: 699–703.
- Li, W., G. Han, Y. Dong, A. Ishimatsu, B. D. Russell & K. Gao, 2015. Combined effects of short-term ocean acidification and heat shock in a benthic copepod *Tigriopus japonicus* Mori. *Marine Biology* 162: 1901–1912.
- Liu, W. & M. He, 2012. Effects of ocean acidification on the metabolic rates of three species of bivalve from southern coast of China. *Chinese Journal of Oceanology and Limnology* 30: 206–211.
- Mathieu, S., D. Sylvain, F. Walden, E. Catapane, and M. Carroll. 2014. GABA is an inhibitory neurotransmitter in ganglia of the bivalve mollusc, *Crassostrea virginica*. *The FASEB Journal* 28: Supplement 1059.4.
- Mazerolle, M. J. 2017. Model selection and multimodel inference based on (Q)AIC(c). <https://cran.r-project.org/web/packages/AICcmodavg/index.html> (last accessed 30 July 2017)
- Melzner, F., M. A. Gutowska, M. Langenbuch, S. Dupont, M. Lucassen, M. C. Thorndyke, M. Bleich & H.-O. Pörtner, 2009. Physiological basis for high CO<sub>2</sub> tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* 6: 2313–2331.
- Michaelidis, B., C. Ouzounis, A. Palaras & H.-O. Pörtner, 2005. Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 293: 109–118.
- Miles, H., S. Widdicombe & J. I. Spicer, 2007. Effects of anthropogenic seawater acidification on acid-base balance in the sea urchin *Psammechinus miliaris*. *Marine Pollution Bulletin* 54: 89–96.
- Morley, S. A., C. C. Suckling, M. S. Clark, E. L. Cross & L. S. Peck, 2016. Long-term effects of altered pH and temperature on the feeding energetics of the Antarctic sea urchin, *Sterechinus neumayeri*. *Biodiversity* 17: 34–45.
- Navarro, J. M., R. Torres, K. Acuña, C. Duarte, P. H. Manríquez, M. A. Lardies, N. A. Lagos, C. Vargas & V. Aguilera, 2013. Impact of medium-term exposure to elevated pCO<sub>2</sub> levels on the physiological energetics of the mussel *Mytilus chilensis*. *Chemosphere* 90: 1242–1248.
- Navarro, J. M., C. Duarte, P. H. Manríquez, M. A. Lardies, R. Torres, K. Acuña, C. A. Vargas & N. A. Lagos, 2016. Ocean warming and elevated carbon dioxide: multiple stressor impacts on juvenile mussels from southern Chile. *ICES Journal of Marine Science* 73: 764–771.
- Noisette, F., F. Bordeyne, D. Davoult & S. Martin, 2016. Assessing the physiological responses of the gastropod *Crepidula fornicata* to predicted ocean acidification and warming. *Limnology and Oceanography* 61: 430–444.
- Norman, S. 2012. The temperature dependence of ectotherm consumption. MSc thesis, Umeå Universitet, Umeå, Sweden. 13 pp. <http://www.diva-portal.org/smash/get/diva2:588173/FULLTEXT01.pdf> (last accessed 08 August 2017).
- Orr, J. C., V. J. Fabry, O. Aumont, et al., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437: 681–686.
- Palmer, A. R., 1992. Calcification in marine molluscs: how costly is it? *Proceedings of the National Academy of Sciences of the USA* 89: 1379–1382.
- Pan, T. C. F., S. L. Applebaum & D. T. Manahan, 2015. Experimental ocean acidification alters the allocation of metabolic energy. *Proceedings of the National Academy of Sciences of the USA* 112: 4696–4701.
- Pedersen, S. A., O. J. Håkedal, I. Salaberria, et al., 2014. Multigenerational exposure to ocean acidification during food limitation reveals consequences for copepod scope for growth and vital rates. *Environmental Science and Technology* 48: 12275–12284.
- Pepin, P., D. Robert, C. Bouchard, J. F. Dower, M. Falardeau, L. Fortier, G. P. Jenkins, V. Leclerc, K. Levesque, J. K. Llopiz, M. G. Meekan, H. M. Murphy, M. Ringuette, P. Sirois & S. Sponaugle, 2014. Once upon a larva: revisiting the relationship between feeding success and growth in fish larvae. *ICES Journal of Marine Science* 72: 359–373.
- Pihl, L., S. P. Baden, R. J. Diaz & L. C. Schaffner, 1992. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology* 108: 349–360.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar. 2017. nlme: linear and nonlinear mixed effects models. <https://CRAN.R-project.org/package=nlme> (last accessed 30 July 2017)
- Poore, A. G., A. Graba-Landry, M. Favret, H. S. Brennan, M. Byrne & S. A. Dworjanyn, 2013. Direct and indirect effects of ocean acidification and warming on a marine plant-herbivore interaction. *Oecologia* 173: 1113–1124.
- Pörtner, H.-O., 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Marine Ecology Progress Series* 373: 203–218.
- R Development Core Team, 2016. *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Ramajo, L., N. Marbà, L. Prado, S. Peron, M. A. Lardies, A. B. Rodriguez-Navarro, C. A. Vargas, N. A. Lagos & C. M. Duarte, 2016a. Biominalization changes with food supply confer juvenile scallops (*Argopecten purpuratus*) resistance to ocean acidification. *Global Change Biology* 22: 2025–2037.
- Ramajo, L., E. Pérez-Léon, I. E. Hendriks, N. Marbà, D. Krause-Jensen, M. K. Sejr, M. E. Bilcher, N. A. Lagos, Y. S. Olsen & C. M. Duarte, 2016b. Food supply confers calcifiers



- resistance to ocean acidification. *Scientific Reports* 6: 19374.
- Ries, J. B., A. L. Cohen & D. C. McCorkle, 2009. Marine calcifiers exhibit mixed responses to CO<sub>2</sub>-induced ocean acidification. *Geology* 37: 1131–1134.
- Rossoll, D., R. Bermúdez, H. Hauss, K. G. Schula, U. Riebesell, U. Sommer & M. Winder, 2012. Ocean acidification-induced food quality deterioration constrains trophic transfer. *PLoS ONE* 7: e34737.
- Runge, J. A., D. M. Fields, C. R. S. Thompson, S. D. Shema, R. M. Bjelland, C. M. F. Durif, A. B. Skiftesvik & H. I. Browman, 2016. End of the century CO<sub>2</sub> concentrations do not have a negative effect on vital rates of *Calanus finmarchicus*, an ecologically critical planktonic species in North Atlantic ecosystems. *ICES Journal of Marine Science* 73: 937–950.
- Russell, B. D., S. D. Connell, H. S. Findlay, K. Tait, S. Widdicombe & N. Mieszkowska, 2013. Ocean acidification and rising temperatures may increase biofilm primary productivity but decrease grazer consumption. *Philosophical Transactions of the Royal Society B* 368: 20120438.
- Saba, G. K., O. Schofield, J. J. Torres, E. H. Ombres & D. K. Steinberg, 2012. Increased feeding and nutrient excretion of adult Antarctic krill, *Euphausia superba*, exposed to enhanced carbon dioxide (CO<sub>2</sub>). *PLoS ONE* 7: e22224.
- Sanford, E., 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integrative and Comparative Biology* 42: 881–891.
- Sanford, E., B. Gaylord, A. Hettinger, E. A. Lenz, E. Meyer & T. M. Hill, 2014. Ocean acidification increases the vulnerability of native oysters to predation by invasive snails. *Proceedings of the Royal Society B: Biological Sciences* 281: 20132681.
- Schoepf, V., A. G. Grottoli, M. E. Warner, W. J. Cai, T. F. Melman, K. D. Hoadley, D. T. Pettay, X. Hu, Q. Li, H. Xu & Y. Wang, 2013. Coral energy reserves and calcification in a high-CO<sub>2</sub> world at two temperatures. *PLoS ONE* 8: e75049.
- Secretariat of the Convention on Biological Diversity. 2009. Scientific synthesis of the impacts of ocean acidification on marine biodiversity, Technical Series No. 46. Montreal, Canada. <https://www.cbd.int/doc/publications/cbd-ts-46-en.pdf> (last accessed 02 August 2017).
- Shumway, S. W., 1977. Effect of salinity fluctuation on the osmotic pressure and Na<sup>+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> ion concentrations in the hemolymph of bivalve molluscs. *Marine Biology* 41: 153–177.
- Small, D. P., P. Calosi, D. Boothroyd, S. Widdicombe & J. I. Spicer, 2016. The sensitivity of the early benthic juvenile stage of the European lobster *Homarus gammarus* (L.) to elevated pCO<sub>2</sub> and temperature. *Marine Biology* 163: 53.
- Smith, J. N., G. De'ath, C. Richter, A. Cornils, J. M. Hall-Spencer & K. E. Fabricius, 2016. Ocean acidification reduces demersal zooplankton that reside in tropical coral reefs. *Nature Climate Change* 6: 1124–1129.
- Stapp, L. S., J. Thomsen, H. Schade, C. Bock, F. Melzner, H. O. Pörtner & G. Lannig, 2017. Intra-population variability of ocean acidification impacts on the physiology of Baltic blue mussels (*Mytilus edulis*): integrating tissue and organism response. *Journal of Comparative Physiology B* 187: 529–543.
- Stevens, P. M., 1987. Response of excised gill tissue from the New Zealand scallop *Pecten novaezelandiae* to suspended silt. *New Zealand Journal of Marine and Freshwater Research* 21: 605–614.
- Stumpp, M., J. Wren, F. Melzner, M. C. Thorndyke & S. T. Dupont, 2011. CO<sub>2</sub> induced seawater acidification impacts sea urchin larval development I: elevated metabolic rates decrease scope for growth and induce developmental delay. *Comparative and Biochemical Physiology Part A: Molecular and Integrative Physiology* 160: 331–340.
- Stumpp, M., M. Hu, I. Casties, R. Saborowski, M. Bleich, F. Melzner & S. Dupont, 2013. Digestion in sea urchin larvae impaired under ocean acidification. *Nature Climate Change* 3: 1044–1049.
- Sui, Y., H. Kong, X. Huang, et al., 2016. Combined effects of short-term exposure to elevated CO<sub>2</sub> and decreased O<sub>2</sub> on the physiology and energy budget of the thick shell mussel *Mytilus coruscus*. *Chemosphere* 155: 207–216.
- Sunday, J. M., P. Calosi, S. Dupont, P. L. Munday, J. H. Stillmon & T. B. H. Reusch, 2014. Evolution in an acidifying ocean. *Trends in Ecology and Evolution* 29: 117–125.
- Talmage, S. C. & C. J. Gobler, 2010. Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proceedings of the National Academy of Sciences of the USA* 107: 17246–17251.
- Tate, R. D., K. Bekendorff, R. Ab Lah & B. P. Kelaher, 2017. Ocean acidification and warming impacts the nutritional properties of the predatory whelk, *Dicathais orbita*. *Journal of Experimental Marine Biology and Ecology* 493: 7–13.
- Thomsen, J., I. Casties, C. Pansch, A. Körtzinger & F. Melzner, 2013. Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. *Global Change Biology* 19: 1017–1027.
- Thor, P. & E. O. Oliva, 2015. Ocean acidification elicits different energetic responses in an Arctic and a boreal population of the copepod *Pseudocalanus acuspes*. *Marine Biology* 162: 799–807.
- Towle, E. K., I. C. Enochs & C. Langdon, 2015. Threatened Caribbean coral is able to mitigate the adverse effects of ocean acidification on calcification by increasing feeding rate. *PLoS ONE* 10: e0123394.
- Tresguerres, M. & T. J. Hamilton, 2017. Acid-base physiology, neurobiology and behaviour in relation to CO<sub>2</sub>-induced ocean acidification. *Journal of Experimental Biology* 220: 2136–2148.
- Vargas, C. A., M. de la Hoz, V. Aguilera, et al., 2013. CO<sub>2</sub>-driven ocean acidification reduces larval feeding efficiency and changes food selectivity in the mollusk *Concholepas concholepas*. *Journal of Plankton Research* 35: 1059–1068.
- Vargas, C. A., V. M. Aguilera, V. San Martín, P. H. Manríquez, J. M. Navarro, C. Duarte, R. Torres, M. A. Lardies & N. A. Lagos, 2015. CO<sub>2</sub>-driven ocean acidification disrupts the filter feeding behavior in Chilean gastropod and bivalve species from different geographic localities. *Estuaries and Coasts* 38: 1163–1177.
- Ventura, A., S. Schulz & S. Dupont, 2016. Maintained larval growth in mussel larvae exposed to acidified undersaturated seawater. *Scientific Reports* 6: 23728.



- Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* 36: 1–48.
- Waldbusser, G. G., B. Hales, C. J. Langdon, B. A. Haley, P. Schrader, E. L. Brunner, M. W. Gray, C. A. Miller, I. Gimenez & G. Hutchinson, 2015. Ocean acidification has multiple modes of action on bivalve larvae. *PLoS ONE* 10: e0128376.
- Wallace, R. B., H. Baumann, J. S. Grear, R. C. Aller & C. J. Gobler, 2014. Coastal ocean acidification: the other eutrophication problem. *Estuarine, Coastal and Shelf Science* 148: 1–13.
- Waller, J. D., R. A. Wahle, H. McVeigh & D. M. Fields, 2016. Linking rising  $p\text{CO}_2$  and temperature to the larval development and physiology of the American lobster (*Homarus americanus*). *ICES Journal of Marine Science* 74: 1210–1219.
- Wang, Y., L. Li, M. Hu & W. Lu, 2015. Physiological energetics of the thick shell mussel *Mytilus coruscus* exposed to seawater acidification and thermal stress. *Science of the Total Environment* 514: 261–272.
- Watson, S.-A., S. Lefevre, M. I. McCormick, P. Domenici, G. E. Nilsson & P. L. Munday, 2014. Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels. *Proceedings of the Royal Society B* 281: 20132377.
- Watson, S.-A., J. B. Fields & P. L. Munday, 2017. Ocean acidification alters predator behaviour and reduces predation rate. *Biology Letters* 13: 20160797.
- Wittman, A. C. & H.-O. Pörtner, 2013. Sensitivities of extant animal taxa to ocean acidification. *Nature Climate Change* 3: 995–1001.
- Wood, H. L., J. I. Spicer & S. Widdicombe, 2008. Ocean acidification may increase calcification rates, but at a cost. *Proceedings of the Royal Society B: Biological Sciences* 275: 1767–1773.
- Wong, W. H. & S. G. Cheung, 2001. Feeding rates and scope for growth of green mussels, *Perna viridis* (L.) and their relationship with food availability in Kat O. Hong Kong. *Aquaculture* 193: 123–137.
- Wu, F., T. Wang, S. Cui, Z. Xie, S. Dupont, J. Zeng, H. Gu, H. Kong, M. Hu, W. Lu & Y. Wang, 2017. Effects of seawater pH and temperature on foraging behavior of the Japanese stone crab *Charybdis japonica*. *Marine Pollution Bulletin* 120: 99–108.
- Xu, X., F. Yang, L. Zhao & X. Yan, 2016. Seawater acidification affects the physiological energetics and spawning capacity of the Manila clam *Ruditapes philippinarum* during gonadal maturation. *Comparative and Biochemical Physiology Part A: Molecular and Integrative Physiology* 196: 20–29.
- Yuan, X., S. Shao, X. Yang, D. Yang, Q. Xu, H. Zong & S. Liu, 2016. Bioenergetic trade-offs in the sea cucumber *Apostichopus japonicus* (Echinodermata: Holothuroidea) in response to  $\text{CO}_2$ -driven ocean acidification. *Environmental Science and Pollution Research* 23: 8453–8461.
- Zhang, H., P. K. S. Shin & S. G. Cheung, 2015. Physiological responses and scope for growth upon medium-term exposure to the combined effects of ocean acidification and temperature in a subtidal scavenger *Nassarius conoidalis*. *Marine Environmental Research* 106: 51–60.