

Experimental assessments of marine species sensitivities to ocean acidification and co-stressors: how far have we come?¹

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Abstract: Experimental studies assessing the potential impacts of ocean acidification on marine organisms have rapidly expanded and produced a wealth of empirical data over the past decade. This perspective examines four key areas of transformative developments in experimental approaches: (1) methodological advances; (2) advances in elucidating physiological and molecular mechanisms behind observed CO₂ effects; (3) recognition of short-term CO₂ variability as a likely modifier of species sensitivities (Ocean Variability Hypothesis); and (4) consensus on the multistressor nature of marine climate change where effect interactions are still challenging to anticipate. No single experiment allows predicting the fate of future populations. But sustaining the accumulation of empirical evidence is critical for more robust estimates of species reaction norms and thus for enabling better modeling approaches. Moreover, advanced experimental approaches are needed to address knowledge gaps including changes in species interactions and intraspecific variability in sensitivity and its importance for the adaptation potential of marine organisms to a high CO₂ world.

Key words: Ocean Variability Hypothesis, ocean warming, acidification, oxygen decline.

Résumé : Les études expérimentales qui évaluent les impacts potentiels de l'acidification des océans sur les organismes marins ont rapidement pris de l'ampleur et produit une abondance de données empiriques au cours de la dernière décennie. Le présent article se penche sur quatre domaines clés d'avancées transformatives dans les approches expérimentales, à savoir : (1) les avancées méthodologiques, (2) les avancées dans l'élucidation des mécanismes physiologiques et moléculaires qui sous-tendent les effets observés du CO₂, (3) la reconnaissance de la variabilité à court terme du CO₂ comme modificateur probable de la sensibilité des espèces (hypothèse de la variabilité des océans) et (4) un consensus sur le fait que les changements climatiques marins sont source de différents facteurs de stress, de sorte qu'il demeure difficile d'anticiper les interactions d'effets. Aucune expérience ne permet à elle seule de prédire le destin de populations futures, mais il est d'importance capitale de poursuivre l'accumulation de preuves empiriques pour produire des estimations plus robustes des normes de réaction des espèces et ainsi permettre de meilleures approches de modélisation. Des approches expérimentales avancées sont en outre nécessaires pour combler des manques de connaissances notamment sur les modifications des interactions d'espèces et la variabilité intraspécifique de la sensibilité et son importance pour le potentiel d'adaptation d'organismes marins à un monde riche en CO₂. [Traduit par la Rédaction]

Mots-clés : hypothèse de la variabilité des océans, réchauffement des océans, acidification, appauvrissement en oxygène.

The challenge of experimentally addressing marine climate change

Anthropogenic climate change has been a scientific consensus for decades, but its reality is coming into ever sharper focus with each new data trove that we collect on the earth's climate and biosphere (IPCC 2014; Shepherd et al. 2018). Excessive carbon dioxide (CO₂) emissions have intensified the earth's greenhouse effect, resulting in land and ocean warming (Mitchell 1989). Warming oceans decline in oxygen content and stratify more (Levin and Breitburg 2015; Breitburg et al. 2018), whereas increased CO₂ dissolution causes ocean acidification (Doney et al. 2009). The problem is regionally exacerbated by anthropogenic nutrient loads (eutrophication) stimulating primary production and successive microbial respiration (Diaz and Rosenberg 2008; Cloern et al. 2016), causing metabolic oxygen depletion and acidification in coastal habitats (Cai et al. 2011; Wallace et al. 2014;

Gobler and Baumann 2016). Ocean warming, acidification, and oxygen decline therefore comprise the main concurrent symptoms of marine climate change (Pörtner 2012; Baumann 2016).

There is no doubt that marine climate change will profoundly impact marine life in ways that are of concern to human food security, well-being, and places to inhabit. But which species exactly will thrive and which will decline? Which will genetically adapt? Will ecosystems become less productive or resilient? None of these questions can presently be answered with confidence, given the large inherent uncertainties in forecasts of nonlinear population and ecosystem responses and the systemic lack of controls, replication, and the immediate ability to falsify predictions, which challenge the scientific method. The difficulties at times elicit extreme notions — fatalism, naiveté, or cynicism — three fallacies that must be avoided. Fatalism can emerge when pioneering research implies the potential for broad, devastating impacts (All is lost!) and such messages then reinforce themselves in

Received 12 July 2018. Accepted 27 November 2018.



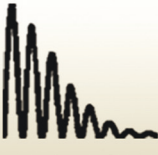

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¹This review is one of a series of invited papers arising from the symposium "Aquatic environments and organisms in transition" that was co-sponsored by the Canadian Society of Zoologists and the *Canadian Journal of Zoology* and held during the Annual Meeting of the Canadian Society of Zoologists at Memorial University of Newfoundland, St. John's, Newfoundland, 7–11 May 2018.

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Fig. 1. Overview of the discussed major advances and challenges in marine climate change experiments. Color version online.

Advances		Challenges
	<p>Best practices for CO₂ manipulation, measurements, reporting</p> <p>Identification of confounding factors</p> <p>Multiple life stages and generations important, carry-over effects</p>	<p>Scale and realism of experimental designs, pseudo-replication</p> <p>Multispecies experiments, indirect effects</p> <p>Field and long-term experiments</p>
Methods		
	<p>Behavioral effects in fish due to GABAA receptor depolarization</p> <p>Metabolic costs of acid-base regulation to high CO₂ small</p> <p>Physiological frameworks, aerobic performance, ATP</p>	<p>Transcriptomic, proteomic up-/down-regulation</p> <p>Trade-offs of CO₂ acclimation</p> <p>Selection under high CO₂</p>
Mechanisms		
	<p>CO₂ varies naturally in time and space, largely due to ecosystem metabolism/upwelling</p> <p>Likely influences species CO₂ sensitivities</p> <p>Potential for local adaptation, transgenerational plasticity</p>	<p>Importance of extreme over average conditions, incorporating CO₂ fluctuations</p> <p>Use of laboratory/commercial broodstocks for sensitivity experiments</p>
Variability		
	<p>Major concurrent stressors = warming, acidification, oxygen loss</p> <p>Synergistic interactions are the norm, not the exception</p> <p>Early life stages are most vulnerable</p>	<p>Mechanistic experiments to study effect interactions vs. realistic experiments to study climate change scenarios</p> <p>Incorporating more than 3 stressors, sequential experimentation</p>
Multistressors		

press releases and public commentary (Browman 2016). This has arguably happened for some groundbreaking experimental assessments on coral, mollusk, and larval fish CO₂ sensitivities (e.g., Orr et al. 2005; Fine and Tchernov 2007; Baumann et al. 2012). However, subsequent studies have since broadened the empirical database, and when more complex and often contradictory patterns emerged (Busch et al. 2015), some have questioned the threat altogether (Don't worry!). Yet naiveté is as unhelpful as the cynic notion that all approaches have inherent shortcomings and answers are therefore elusive (Nothing we can do!). In reality, not all is lost, but there is reason to worry, and science has tools to address the problem. As the past decade of experimental, observational, and modeling approaches has demonstrated, by avoiding extremes, science has advanced our understanding of potential species and ecosystem responses to marine climate change. Although considerable knowledge gaps remain, this perspective focuses on the progress made, specifically in the field of experimental ocean acidification research.

Most studies addressing acidification, warming, and low oxygen effects in marine organisms have taken an experimental approach (Browman 2016). Its central premise is to trade environmental realism (e.g., CO₂ variability, species interactions) for environmental control (Sommer 2012) to obtain basal information

on CO₂ sensitive vs. CO₂ tolerant traits, life stages, and species and to elucidate mechanisms that cause observed effects (Boyd et al. 2018; Snyder et al. 2018). Experiments are therefore critical stepping-stones on the way to higher order questions such as community effects and adaptive evolution (Pfister et al. 2014; Sunday et al. 2014; Gaylord et al. 2015). The considerable progress made by experiments is evident from the large number of recent reviews and meta-analyses, e.g., on multistressor experiments (Byrne and Przeslawski 2013; Przeslawski et al. 2015; Boyd et al. 2018), acidification effects on fish (Ashur et al. 2017; Esbaugh 2018; Cattano et al. 2018), CO₂ × temperature interactions (Harvey et al. 2013; Kroeker et al. 2013; Lefevre 2016), and CO₂ × O₂ effects (Gobler and Baumann 2016). Thus, past decades have amassed empirical data sets that can now be mined for overarching patterns, however, incomplete yet. Importantly, this work in progress needs to be sustained, based on the lessons learned.

I suggest that transformative progress over the past decade has occurred in four key areas (Fig. 1). A first area contains methodological advances that include standardization and identification of confounding factors. A second area encompasses advances in understanding physiological and molecular mechanisms of CO₂ sensitivity in marine organisms. The third area is comprised by the recognition that short-term variability in environmental CO₂

conditions likely modifies species sensitivities to acidification. This involves intriguing plasticity in responses to highly dynamic environments and the general expectation of changing vulnerabilities across spatial CO₂ variability gradients (Ocean Variability Hypothesis). The fourth area contains the broad consensus on marine climate change as a multistressor problem and the progress in assessing stressor interactions.

Key area 1: methodological advances

CO₂ manipulation and reporting

To ensure comparability of studies, experimental researchers have strived to standardize the terminology and practices of CO₂ manipulation, measurement, and reporting while further improving husbandry methods of model organisms (e.g., Gattuso and Hansson 2011; Riebesell et al. 2011). It is now standard that experiments manipulate seawater pH only by CO₂ dissolution (not acid) and that the full experimental water chemistry is assessed, calculated (e.g., via CO₂SYN), and reported in the primary literature. These developments have been aided by parallel refinements of carbon chemistry kinetics (Dickson and Millero 1987), particularly for brackish water systems (Millero 2010), and recent inter-laboratory calibration studies for measurements of alkalinity and pCO₂ (Bockmon and Dickson 2015). Better consensus also emerged on terminology, e.g., by more clearly distinguishing the long-term process of ocean acidification from experimental assessments of species sensitivities to elevated CO₂ conditions (Browman 2016; McElhany 2017). Regarding CO₂ levels, there is now principal agreement that treatments should reflect plausible future levels in aquatic habitats. For example, aquaculture experiments over the past 50 years often tested pCO₂ levels of 10 000 – 50 000 µatm on juvenile and adult fishes (Ishimatsu et al. 2008), which is unrealistic in the context of ocean acidification. Rather, pCO₂ levels of ~2000 µatm have emerged as a common upper benchmark, based largely on Caldeira and Wickett's (2003) seminal estimate of worst-case pCO₂ concentrations in the average surface ocean by the year 2300 (Riebesell et al. 2011). End-of-this-century treatments of ~1000 µatm are also commonly employed. However, one issue with such open-ocean levels is that most marine organisms do not live there; instead, they mostly inhabit coastal shelf and near-shore environments (Costanza et al. 1997; Hendriks et al. 2010) with profoundly different CO₂ baselines and fluctuations (key area 3; Vargas et al. 2017). Due to the declining buffering capacity of oceans (Revelle factor), these fluctuations will further intensify and thus expose many organisms to critical CO₂ levels earlier than previously predicted (Shaw et al. 2013; McNeil and Sasse 2016). Hence, there is now consensus that upper realistic pCO₂ levels in experiments need to be flexible and cognizant of the differing acidification trajectories in marine habitats (Salisbury and Jönsson 2018; Busch et al. 2015; Vargas et al. 2017).

Factors confounding CO₂ experiments

Experimenters have also identified factors that can bias CO₂ sensitivity assessments in marine organisms. Adverse CO₂ effects on coral calcification, for example, appear to depend on experimental light levels that thus need to be controlled and reported (Suggett et al. 2013). Food availability has been shown to affect CO₂ sensitivities across taxa including pteropods (Seibel et al. 2012), bivalves (Thomsen et al. 2013), and fish (Gobler et al. 2018; Stiasny et al. 2018). In the latter, high CO₂ is often believed to increase metabolic costs of acid-base regulation and therefore to reduce growth (key area 2; Heuer and Grosell 2016), but firm empirical support for this hypothesis is lacking (Esbaugh 2018; Hurst et al. 2017; Cattano et al. 2018). It is possible that these costs are too small to be detectable in short-term exposures (Baumann et al. 2018a). Another reason could be that fish larvae are often fed in excess (ad libitum), which reduces their overall mortality but also allows survivors to compensate for increased metabolic costs by

increased food consumption. Hence controlling or accounting for experimental feeding conditions seems critical for comparable estimates of CO₂ effects. Inadvertent buildup of nitrogenous waste in rearing containers can also confound estimates, because ammonia toxicity to fish and other organisms generally increases with pH (Randall and Tsui 2002), thus affecting predominantly the control over high CO₂ (low pH) treatments. Largely unresolved, however, are frequent concerns about pseudoreplication in CO₂ exposure experiments (e.g., shared water sources, enclosures, founding populations). How exactly this issue confounds empirical estimates remains poorly quantified, and there is currently no clear consensus on acceptable compromises between the most rigorous experimental designs and those that are logistically feasible.

Experiments across multiple life stages and generations

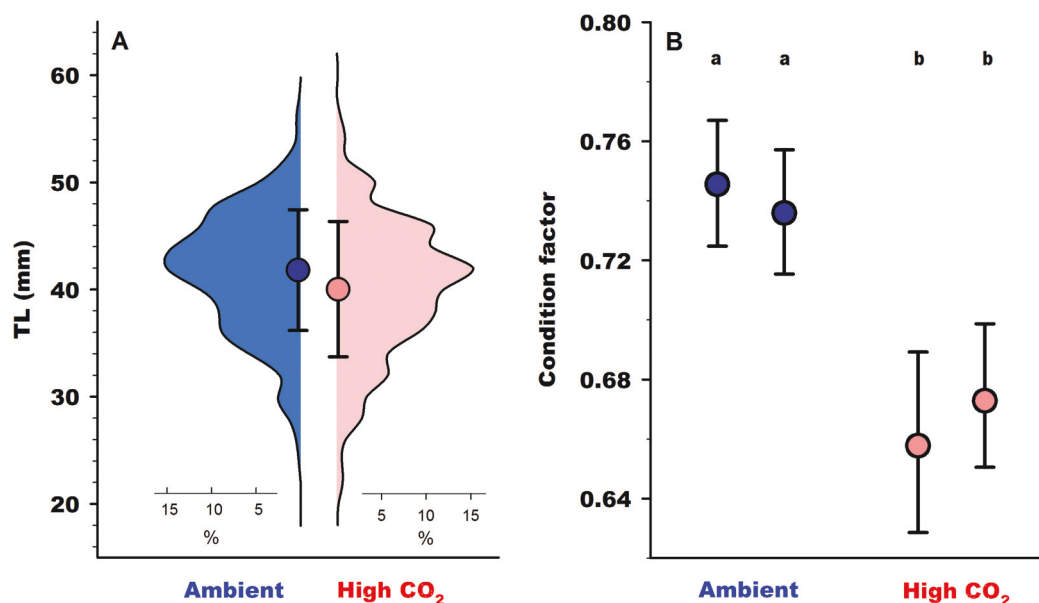
One of the most robust patterns across taxa is the general decrease in CO₂ sensitivity from early life to juvenile and adult ontogenetic stages (Harvey et al. 2013; Przeslawski et al. 2015; Cattano et al. 2018). This may explain why a majority of published experiments have focused on short-term exposures and the most vulnerable early life stages (embryos, larvae). However, evolving CO₂ rearing systems and better husbandry methods now also allow longer term experiments that span multiple life stages, whole life cycles, and even generations. Although these approaches are still scarce, logistically challenging, and feasible only for select model species, they have clearly highlighted the potential for carry-over effects and transgenerational acclimation, both of which alter our overall assessment of species CO₂ sensitivities. For example, work on the Atlantic silverside (*Menidia menidia* (Linnaeus, 1766)), an important nearshore forage fish along the North American Atlantic coast, demonstrated that high CO₂ environments can indeed incur growth costs (Figs. 2A, 2B), but this effect was only detectable after rearing large numbers of individuals from fertilization to late juvenile or adult stages under non-excess food conditions (Murray et al. 2017).

Conversely, when CO₂ experiments have included parental generations, offspring CO₂ tolerance frequently increased (Munday 2014); a form of transgenerational plasticity (TGP) via maternal provisioning or epigenetic modifications that is surprisingly well documented for many stressors and taxa (Jablonka and Raz 2009; Salinas and Munch 2012; Salinas et al. 2013; Munday 2014). TGP may allow species in highly dynamic coastal environments to precondition their offspring to seasonally changing CO₂ conditions (key area 3; Murray et al. 2014). Moreover, it may provide a short-term refuge to the increasing stressors of marine climate change. Unfortunately, the ubiquity of TGP may also comprise yet another confounding factor for experiments, which by definition seek to assess CO₂ sensitivities of species as they currently exist in the wild. But when experimental organisms are obtained from commercial or laboratory brood stocks (Baumann et al. 2012; Chambers et al. 2014; Bromhead et al. 2015; Stiasny et al. 2016), they are likely genetically less diverse and the parental generation at least partially experienced artificial temperature, CO₂, light, and feeding conditions (Baumann et al. 2018b). Via TGP, these parental conditions influence offspring CO₂ sensitivities, and this additional uncertainty needs to be more clearly acknowledged and then accounted for in scaled-up models.

Key area 2: mechanisms underlying CO₂ effects in marine organisms

The question what exactly high pCO₂ exposure does to marine organisms is central to experiments, as only a firm mechanistic understanding allows correct interpretations of observed CO₂ effects, improves modeling approaches, or reveals mitigating pathways such as acclimation or evolutionary adaptation. Physiologists have long understood that marine metazoans — unlike

Fig. 2. Long-term growth costs of high CO₂ conditions in the Atlantic silverside (*Menidia menidia*). (A) Violin plot of total length (TL) frequency distributions of juveniles reared from fertilization to 122 days post hatch under ambient condition (blue (dark gray in print); ~500 μ atm, $n = 1025$) vs. high CO₂ condition (red (light gray in print); ~2300 μ atm, $n = 1100$) (data from Murray et al. 2017). Symbols denote mean \pm SD. (B) Condition factor K ($10^5 \times \text{wet mass} / \text{TL}^{2.944}$, where wet mass is measured in grams (g) and TL is measured in millimetres (mm)) of adults reared in duplicates from fertilization to 280 days post hatch under ambient condition (blue (dark gray in print); ~500 μ atm, $n = 155$) vs. high CO₂ condition (red (light gray in print); ~2300 μ atm, $n = 132$). Symbols denote mean \pm 95% bootstrapped confidence intervals. Color version online.



single-cell organisms — have extracellular fluids that they control to ensure the proper functioning of pH-sensitive, metabolic enzymes (Fabry et al. 2008; Pörtner 2008). Regulatory capacity appears to increase from sessile to more mobile taxa (Melnzer et al. 2009) and generally involves either responses to accelerate the off-gassing of excessive CO₂ (e.g., by increased ventilation) or responses to increase the buffering capacity of extracellular fluids (e.g., by increasing bicarbonate concentrations) (Esbaugh 2018). As active swimmers, juvenile and adult fishes are particularly effective at both CO₂ and acid–base regulation so that even a doubling of environmental $p\text{CO}_2$ may only lead to a 10% $p\text{CO}_2$ increase in their blood (Melnzer et al. 2009; Heuer and Grosell 2014, 2016). This ability is likely further enhanced in species occurring in highly CO₂ variable habitats (key area 3) and explains why most juvenile and adult fishes tolerate even extreme CO₂ levels on time scales of weeks to months (Ishimatsu et al. 2004), whereas early life stages that still develop acid–base competency may not. It also explains why most observed CO₂ effects in fish involve sublethal, downstream responses related to physiological CO₂ or pH compensation (e.g., behavior, metabolism, growth, aerobic scope, overcalcification), not direct acidosis. For example, the consistently observed overcalcification of fish otoliths under high CO₂ conditions likely results from increased CO₃²⁻ concentrations in the endolymph fluid of the inner ear caused by increased bicarbonate (HCO₃⁻) pH buffering of the blood (Checkley et al. 2009; Hurst et al. 2012; Bignami et al. 2013; Schade et al. 2014).

Our mechanistic understanding of behavioral impairments in fish larvae has arguably progressed the most, thanks to sustained empirical assessments combined with neurophysiological approaches (reviewed by Ashur et al. 2017). These revealed that impairments of chemical, auditory, and visual senses in fish can already manifest in response to small increases in ambient $p\text{CO}_2$ (from 400 to 700–800 μ atm) and often result in a large suite of maladaptive behaviors such as the inability to distinguish chemical cues from predators or preferable settlement habitats (Munday et al. 2009, 2010), to hear nearby reefs (Simpson et al. 2011; Castro et al. 2017), or to visually assess predation risk (Ferrari et al. 2012a). Increased anxiety (Hamilton et al. 2014), lateralization (Domenici

et al. 2012), and reduced learning ability have also been observed (Ferrari et al. 2012b; Jutfelt et al. 2013). The underlying mechanism for these impairments is likely a malfunction of γ -aminobutyric acid_A (GABA_A), which is the primary inhibitory neurotransmitter receptor in vertebrate brains (Ashur et al. 2017). Its crucial, inhibitory function results from membrane hyperpolarization. But when fish increase blood HCO₃⁻ to buffer against decreasing pH due to elevated $p\text{CO}_2$, the ionic shift results in depolarizing rather than hyperpolarizing neuron membranes when GABA binds to GABA_A, causing maladaptive behavior (Nilsson et al. 2012). However, alternative mechanisms almost certainly exist. Recently, behavioral abnormalities of European seabass (*Dicentrarchus labrax* (Linnaeus, 1758)) were shown to result from general impairments of the peripheral olfactory system after high CO₂ exposure, not GABA_A inhibition in the brain (Porteus et al. 2018). In both cases, the deleterious behavior appears to manifest only after prolonged, constant CO₂ exposure (>24 h), whereas most effects are mitigated under more realistic diel CO₂ fluctuations (Jarrold et al. 2017). As with all other traits studied thus far, behavioral CO₂ sensitivities, too, vary even between taxonomically and ecologically similar fish species (Ferrari et al. 2011), and neutral responses are likely more common than currently acknowledged (Jutfelt and Hedgärde 2013).

As an alternative to species-by-species assessments of response traits, physiologists have suggested that experiments test bioenergetic frameworks (Pörtner 2012; Sokolova 2013), because they focus on, e.g., aerobic scope as the affected, fundamental trait (a proxy for the surplus energy available for growth, reproduction, predator avoidance, etc.). For example, the oxygen and capacity limited thermal tolerance (OCLTT) hypothesis stipulates that species-specific and life-stage-specific thermal windows constrain an organism's capacity for aerobic metabolism (Pörtner 2010; Pörtner et al. 2017). In pH conformers (some invertebrates), high CO₂ levels may further reduce these thermal windows by directly depressing the oxygen content of blood and other body fluids or by decreasing the functional capacity of pH-sensitive proteins (e.g., hemoglobin and hemocyanin). On the other hand, pH regulators (e.g., fish) likely respond by increasing ventilation rates,

acid–base regulation, or by activating mechanisms for protection and damage repair, which elevate basal metabolic rate and shrink the aerobic scope. Although intuitive, the OCLTT hypothesis is not universally supported by all available empirical evidence (Jutfelt et al. 2018), given that many ectotherms appear to lack clear thermal optima for aerobic scope (Lefevre 2016), or thermal optima are inconsistent with temperatures experienced in the wild and often fail to align with other thermal reaction norms, e.g., in growth and reproduction (Gräns et al. 2014; Norin et al. 2014). Hence, alternative physiological frameworks that focus instead on food assimilation and (or) stress-induced impacts on the aerobic production of adenosine triphosphate (Sokolova 2013) and protein synthesis (Frieder et al. 2018) are worth exploring more broadly.

Finally, experiments have already begun to make progress in addressing questions beyond acute species CO₂ sensitivities, such as assessing de novo evolution in single-cell organisms (Lohbeck et al. 2012) or quantifying genotypic differences in longer lived metazoans that will determine the evolutionary potential of these organisms. For example, an experiment on purple sea urchin (*Strongylocentrotus purpuratus* (Stimpson, 1857)) larvae demonstrated that high CO₂ conditions led to allelic shifts in the surviving larval population (Pespeni et al. 2013). Others have quantified the heritability of traits such as growth or survival under acidified conditions, generally revealing that CO₂ tolerance has a small but significant genetic component and could therefore evolve (Parker et al. 2011; Malvezzi et al. 2015). In addition, progress with respect to transgenerational acclimation via epigenetic mechanisms or maternal provisioning (Snyder et al. 2018) has suggested that short-term pathways exist for many marine organisms to cope with acidification (Munday 2014; Murray et al. 2014; Thor and Dupont 2015). All recent syntheses agree that acclimation and adaptation represent important frontiers in experimental ocean acidification research, with the potential to change our perception of potentially vulnerable vs. resilient species in a high CO₂ ocean (Munday et al. 2013; Sunday et al. 2014; Boyd et al. 2018).

Key area 3: spatial variability in short-term CO₂ fluctuations

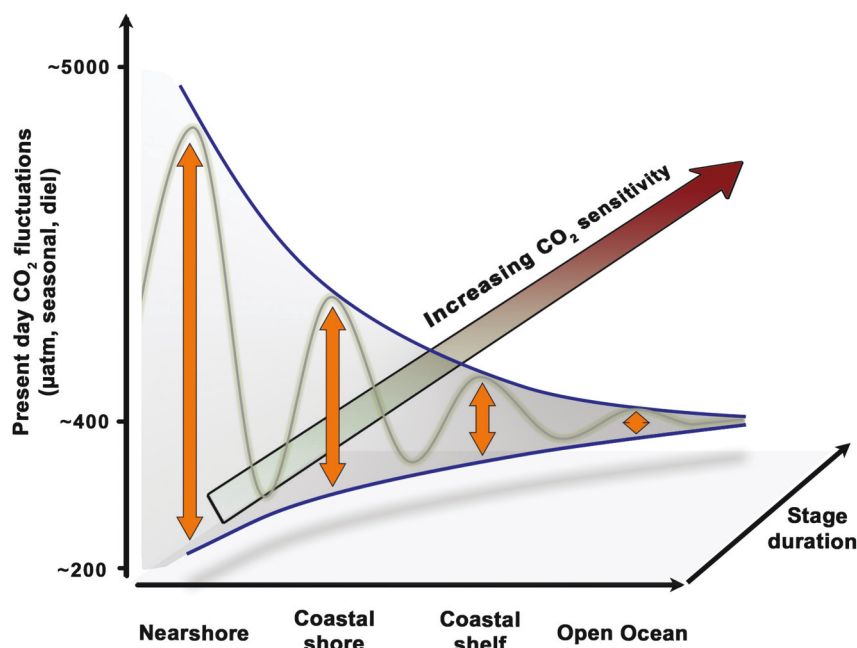
Empirical assessments of CO₂ responses are necessarily limited to a very small fraction of existing marine species, e.g., in marine fish, where only 60 of approximately 20 000 species have been studied so far (~0.3%; Cattano et al. 2018). This means that experiments generally have a broader implicit objective, which is to reveal patterns applicable to other taxonomically or ecologically similar species and thus to provide a basis for inferring community and ecosystem responses to ocean acidification. Unfortunately, the empirical evidence so far suggests that CO₂ sensitivities in marine organisms are intriguingly complex, with examples for negative, neutral (likely underreported; Browman 2016), and positive responses to high CO₂ documented for a large number of traits between ecologically similar or closely related species, populations, and even repeated experiments. For example, direct negative CO₂ effects on fish early life survival have been reported for some but not most studied species (Cattano et al. 2018). Traits such as metabolism, aerobic scope, swimming performance, and growth, which are largely controlled by other abiotic (e.g., temperature, salinity, oxygen) and biotic (food, genes) factors appear to be most heterogeneous in their CO₂ sensitivity (Lefevre 2016; Cattano et al. 2018). Even among the more consistent behavioral and otolith overcalcification responses in fish (Ashur et al. 2017; Cattano et al. 2018), unexplained differences between species exist (Ferrari et al. 2011; Munday et al. 2011; Jutfelt and Hedgärde 2013). Although some variability in experimental outcomes may be attributed to methodological uncertainty (key area 1), the majority of it still deserves exploring beyond broad meta-analytical approaches. An often-invoked claim is that re-

sponses may simply be species-specific, which is unsatisfactory for lacking causation and for its logical but impractical consequence that thousands of additional species would still require testing. Instead, further insights could still come from more explicitly considering species responses against the level of CO₂ variability in their natural environments, a framework related to the more general Climate Variability Hypothesis (e.g., Compton et al. 2007; Markle and Kozak 2018; Ortega-Mayagoitia et al. 2018), but which in the specific context of CO₂ sensitivities I suggest be called Ocean Variability Hypothesis (OVH; Fig. 3).

The OVH is based on the broad recognition that marine habitats differ vastly in the frequency and magnitude of short-term pCO₂ fluctuations (Hofmann et al. 2011; Duarte et al. 2013). These fluctuations can be ephemeral in upwelling regions or in the vicinity of volcanic CO₂ seeps (Hall-Spencer et al. 2008). But for most marine habitats, they follow annual, diel, or tidal cycles caused by changes in net ecosystem metabolism (Odum et al. 1995; Gagliano et al. 2010; Baumann and Smith 2018), where net heterotrophy leads to metabolic acidification (pH decrease) and net autotrophy causes the reverse process, i.e., basification (pH increase). Importantly, this natural CO₂ variability follows a clear spatial pattern, with generally decreasing amplitudes from nearshore to open-ocean environments (Hofmann et al. 2011). In nearshore habitats, where biological productivity is usually highest (Cloern et al. 2016), diel and seasonal CO₂ fluctuations between 200 and 5000 µatm (more than one full pH unit in full strength seawater) are common and more than twice the worst-case, open-ocean pCO₂ increase over the next three centuries (Caldeira and Wickett 2003). With increasing distance from shore, however, the seasonality and metabolic dominance of the marine carbon system dissipates until approaching near-stable pCO₂ conditions year-round in the open ocean (Hofmann et al. 2011; Duarte et al. 2013). This spatial gradient means, first, that the anthropogenic acidification signal strengthens from largely undetectable in nearshore habitats (Duarte et al. 2013) to clearly discernable over decadal time scales in the open ocean (Doney et al. 2009; Lauvset et al. 2015). It also implies that marine organisms are likely adapted to the level of contemporary CO₂ fluctuations in their natural habitats. Assuming that high CO₂ tolerance comes at a cost to organisms, one should therefore expect CO₂ sensitivities to change from tolerant nearshore to more sensitive open-ocean species. Indeed, Vargas et al. (2017) recently showed that CO₂ sensitivities in several Chilean mollusk and copepod species decrease with increasing short-term CO₂ fluctuations in their natural habitat — a first explicit test of the OVH. For fish, this framework has not yet been explicitly tested, although a recent meta-analysis by Cattano et al. (2018) differentiated CO₂ responses between marine fishes from several climatic regions (polar, temperate, subtropical, tropical) or benthic vs. pelagic habitats. Although valuable, such contrasts are still likely to group species from habitats with different baselines of CO₂ variability.

CO₂ sensitivities in marine fish illustrate the potential of OVH (Fig. 3). Early life stages of nearshore species such as three-spined sticklebacks (*Gasterosteus aculeatus* Linnaeus, 1758) (Schade et al. 2014), Atlantic silversides (Baumann et al. 2018b; Murray and Baumann 2018), red drum (*Sciaenops ocellatus* (Linnaeus, 1766)) (Lonthair et al. 2017), or spring-spawning Baltic herring (*Clupea harengus* Linnaeus, 1758) (Franke and Clemmesen 2011) appear generally tolerant of CO₂ levels of 2000 µatm and above with no or very small effects on survival or growth. In Atlantic silversides, years of repeated experimentation documented average reductions in embryo survival by only 10% in response to ~2000 µatm CO₂, and these effects mainly occurred in offspring produced at the beginning or end of the species spawning season (Baumann et al. 2018b). Marine medaka (*Oryzias latipes* (McClelland, 1839)) and sheepshead minnow (*Cyprinodon variegatus* Lacepède, 1803) embryos and larvae appear to tolerate even the most extreme CO₂ levels tested so far (Depasquale et al. 2015; Mu et al. 2015). Al-

Fig. 3. Illustration of the Ocean Variability Hypothesis positing that the CO₂ sensitivity of marine organisms is related to the magnitude of short-term CO₂ fluctuations in their habitat (e.g., from nearshore to open ocean) and length of their early life stage durations. It suggests that the most CO₂ tolerant marine organisms are those that develop fast and (or) in habitats with large contemporary CO₂ fluctuations, whereas the potentially most vulnerable species are those that develop slowly in relatively stable open-ocean habitats. Color version online.



though taxonomically diverse, these examples all represent species that reproduce in very shallow, nearshore waters with likely large short-term CO₂ fluctuations to which they must be adapted.

Slightly greater CO₂ sensitivities, on the other hand, appear to exist for coastal shelf species including Atlantic cod (*Gadus morhua* Linnaeus, 1758) (Stiasny et al. 2016, 2018), summer flounder (*Paralichthys dentatus* (Linnaeus, 1766)) (Chambers et al. 2014), and Senegalese sole (*Solea senegalensis* Kaup, 1858) (Pimentel et al. 2014b), where significant reductions in embryo and larval survival have already been observed in response to 1000–2000 µatm pCO₂. Coral reef fish may also fall under this category, given the diminished but still substantial CO₂ variability in their habitats (Gagliano et al. 2010; Hofmann et al. 2011) and the well-documented behavioral responses to CO₂ levels below 1000 µatm (Ashur et al. 2017). However, direct CO₂-induced survival effects are conspicuously absent in this group (Munday et al. 2011; Welch and Munday 2016), which might be due to interactive effects of development time on early life CO₂ sensitivity. In contrast to higher latitude species, most tropical fish hatch within few days post fertilization and become actively swimming larvae within as little as 1 week. It is possible that offspring in these cases acquire acid–base competency too fast for significant adverse survival effects to accrue. The same caveat applies to the few tested open-ocean species such as yellowfin tuna (*Thunnus albacares* (Bonnaterre, 1788)) (Frommel et al. 2016), dolphinfish (*Coryphaena hippurus* Linnaeus, 1758) (Pimentel et al. 2014a), and yellowtail amberjack (*Seriola lalandi* Valenciennes, 1833) (Munday et al. 2016) that reproduce in relatively CO₂ stable environments and should therefore be most sensitive to high CO₂ conditions. Although there is evidence for lethal and sublethal effects of high CO₂ in these pelagic species (but see Watson et al. 2018), all have fast-developing early life stages that become active piscivores within days post hatch, which requires well-developed acid–base competency (Melzner et al. 2009).

Stage duration may therefore comprise a second important dimension of OVH (Fig. 3). It suggests that the most CO₂ tolerant marine organisms are those that develop fast and (or) in habitats with large contemporary CO₂ fluctuations, whereas the potentially most vulnerable species are those that develop slowly in

relatively stable open-ocean habitats. Unfortunately, at least in marine fish, this latter group remains almost unstudied, but likely includes offshore winter spawners in temperate or high latitude environments that have extended embryonic and larval durations (C.S. Murray, D. Wiley, and H. Baumann, unpublished data). In addition, there are other spatial CO₂ variability gradients beyond the general nearshore–offshore axis that appear equally suitable to test OVH. Such gradients likely exist with depth, as many marine species exhibit distinct daily or ontogenetic vertical migrations (Godø et al. 2009), or with the level of eutrophication in coastal waters. In upwelling regions such as the California Current Large Marine Ecosystem (Kelly et al. 2013) or along the coast of Chile (Vargas et al. 2017), different regions exhibit different levels of ephemeral upwelling and therefore short-term CO₂ variability. Consistent with the hypothesis, a study on purple sea urchin found that offspring from high CO₂ variability regions were less CO₂ sensitive than their conspecifics from low CO₂ variability areas (Kelly et al. 2013).

Key area 4: marine climate change is a multistressor problem

The concurrent rise in ocean temperature and CO₂ or the intensifying co-occurrence of high CO₂ and low oxygen conditions in urban estuaries or oxygen minimum zones (Cai et al. 2011; O’Boyle et al. 2013; Breitburg et al. 2015; Baumann and Smith 2018) are just two of many examples that demand assessments of species sensitivities to stressor combinations. This is necessary given the likelihood that combined stressors elicit quantitatively or qualitatively different effects than the sum of each stressor alone (Breitburg et al. 2015). These stressor interactions may be antagonistic and thus mitigate the overall response; however, the potential for synergistic interactions causing disproportionately adverse effects is the most concerning. For example, early experiments on the hard coral *Stylophora pistillata* Esper, 1797 found that calcification rates increased with CO₂ under control temperatures but decreased at combined high CO₂ and high temperature treatments (Reynaud et al. 2003). A recent CO₂ × O₂ factorial experi-

ment on Atlantic silversides (Depasquale et al. 2015) observed no effects of high CO₂ on early life survival at normoxic treatments, but synergistic survival reductions under low oxygen × high CO₂ treatments. Even in elasmobranchs such as juvenile brown-banded bambooshark (*Chiloscyllium punctatum* Müller and Henle, 1838), both additive and synergistically negative CO₂ × temperature interactions were evident in traits like survival and ventilation rate (Rosa et al. 2014).

The most extensive empirical evidence exists for CO₂ × temperature effects so far, particularly in mollusks, crustaceans, and echinoderms, while less so for marine fish. A pioneering meta-analysis revealed that high CO₂ × temperature conditions appear to have mostly additive effects (no interaction) on early life survival in marine crustaceans, whereas mollusk species are synergistically negatively affected (Harvey et al. 2013). However, a different pattern emerged for another trait, growth, where strong and synergistically negative CO₂ × temperature effects characterized crustaceans, only weakly negative additive effects were found for mollusks, and overall positive effects occurred in echinoderm species. Thus, multistressor responses vary across taxa, stages, and trophic levels, and our current predictive capacity is still in its infancy with respect to where and when they occur. Furthermore, although earlier meta-analyses found synergistic interactions to be less frequent than additive or antagonistic effects (Byrne and Przeslawski 2013; Harvey et al. 2013), a more recent synthesis concluded just the opposite (Przeslawski et al. 2015).

For the combined effects of high CO₂ and low dissolved oxygen, the empirical evidence is much scarcer still and not yet sufficient for conclusive meta-analyses (Gobler and Baumann 2016), despite the universal recognition that these two stressors are tightly coupled in most marine habitats on short and long time scales (Baumann and Smith 2018). An initial review concluded that, individually, low oxygen conditions are more stressful to marine organisms than high CO₂. In combination, the two stressors appear to cause mostly additive negative effects; however, every study to date also found synergistic negative interactions in at least one examined trait (Gobler et al. 2014; Gobler and Baumann 2016; Miller et al. 2016). There is a clear and well-understood need to expand multistressor experiments in this area, including the important addition of testing fluctuating CO₂ × O₂ environments because they are most common in nature and may mitigate or further exacerbate effects.

Importantly, designing multistressor experiments also comes with new and complex challenges, which have recently been comprehensively reviewed by Boyd et al. (2018). The authors found that modern empirical assessments have begun to diverge in scope in two complementary directions. The first group comprises reductionist approaches that gain mechanistic insights into the nature of stressor interactions via full-factorial designs in well-controlled laboratory settings. This comes, however, at the expense of environmental realism both in terms of near-future projections and the lack indirect effects that will ultimately determine ecosystem responses and thus guide policy decisions. Furthermore, factorial designs become rapidly unwieldy if they try to include more than two stressors and more than two exposure levels at the time. Beyond the obvious logistical challenges, difficulties in interpretation and presentation of multistressor observations increase exponentially with design complexity while making spurious patterns more likely. Suggested solutions include sequential testing and then combining of multiple stressors (Boyd et al. 2018), as well as repeating experiments themselves to increase statistical power (Baumann et al. 2018b; Murray and Baumann 2018). A second group of multistressor experiments encompasses mesocosms and field manipulations (Sswat et al. 2018), which trade some environmental control for greater realism to measure overall community effects in response to projections of ocean change (Alsterberg et al. 2013) while consciously ceding the

ability to distinguish between the exact mechanisms behind observed effects. These approaches are often even more logistically challenging and thus allow fewer replicates and reduced statistical power. However, both groups of multistressor approaches are important to sustain (Boyd et al. 2018).

Going forward, refined experiments will continue to contribute important data toward anticipating the impacts of marine climate change, particularly when they include multiple life stages, examine potential carry-over effects, and are focused on traits of known fitness relevance.

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